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PERMEABILITY OF CHITIN IN SOME DIPTEROUS LARVAE AND THE METHOD OF ITS STUDY

BY

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Though the literature on the permeability of the most different plant and animal cells and membranes is enormous, the chitin is hardly studied at all from this point of view. Meanwhile it should be emphasised that because the integument and considerable part of the alimentary tract in Arthropoda are lined with the chitin, to investigate the permeability of the latter would be undoubtedly important for the elucidation of a number of physiological and ecological problems in the indicated animal group.

Larvae of *Chironomus plumosus* L., *Glyptotendipes polytomus* and *Corethra plumicornis* LATR. have been chosen as material for the present research work, in which an attempt is made to discover the ways by which diluted substances penetrate into the body cavity of larvae and to study the typical features of the permeability of their chitin. A special method has been elaborated allowing to study permeability of the chitinous cuticle isolated from its own hypoderm.

COMPARISON OF THE PERMEABILITY OF LARVAE FOR VITAL STAINS.

Many of the vital stains (neutralrot, methylen blue, thionine) are easily accumulated in the larval tissues of *Chironomus plumosus*. That is why they have been used in a number of investigations on the intravital coloration. (PARAT 1928, KOLMER and FLEISCHMANN 1928, KRYUKOVA 1929, SALKIND 1929, 1929 a, etc.)

When studying the influence of oxidy-reducing conditions on the vital coloration of the larvae of *Chironomus plumosus* (1932) the author paid attention to the fact that in some larvae belonging to the same family, e.g.

Glyptotendipes polytomus, it is very difficult to stain the organs if even keeping the larvae for a long period in a comparatively concentrated solution of stain. Similarly PAUSE (1918) has found impossible to stain *Chironomus gregarius* with neutralrot and methylen blue. The larva of *Corethra plumicornis* owing to its unique transparency affords excellent possibilities for the intravital study; but if placed in the solutions of stains in requires enormous efforts to be stained. This circumstance is noticed by KOLMER (1904), FRANKENBERG (1915), NAGEL (1927) and SALKIND.

The experiments carried through by me have shown that the rapidity of the appearance of the stain granules in the tissues of larvae placed in the solutions of basic vital stains depends largely upon pH concentration. The staining is very much quickened by the alkaline reaction of the surrounding solution which fact corresponds with the other authors' data (MCCUTSCHEON and LUCKE 1924). The values given in the subsequent description are obtained in the aqua distillata solutions of about 5.7 pH. Considerable individual fluctuations and the influence of temperature on the time necessary for staining should be noticed, as well.

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The beginning of the neutralrot staining may be discovered in a few hours since having placed the larvae of *Chironomus plumosus* in the 0.04 % solution of the indicated stain at 16—18° C. After some 2—4 hours the accumulation of the neutralrot granules takes place in the fat-body, Malpighian tubes, salivary and pericardial glands and so on; then the granules increase speedily in number and size. Larvae of *Glyptotendipes polytomus* show a little amount of granules in the foremost part of the stomach after some 4—7 hours while in all the remaining organs they are totally absent. In the fat-body, Malpighian tubes, pericardial glands and other organs the stain may be recorded only after 24 or 48 hours, but again in small quantity. A still slower process of staining is observed in *Corethra* larvae, where the first granules also may be seen in the anterior part of the stomach; they appear mostly on the second day of action, or in some individuals still later.

Other basic stains as, e.g., thionin and brilliantscresylblau of 0.03 % concentration also stain the tissues of *Chironomus plumosus* though slower than neutralrot. The attempts failed to stain *Glyptotendipes* larva keeping it 4 days in the solutions of the same concentrations; only a few larvae showed coloration of the anterior part of the mid-gut.

There are several explanations to be accounted for the indicated distinctions in the behaviour of different species towards stains. If the latter principally penetrate through the alimentary canal the distinctions may depend upon differences in the permeability of the intestinal wall; if the latter is identical in all the species dealt with the distinctions may depend upon differences in the entering of the surrounding fluid into the cavity of the intestine. If on the other hand the tissues are coloured by the stains that

have passed through the larval integument it should be concluded that the latter is more permeable in *Chironomus plumosus*, than in *Glyptotendipes polytomus* and *Corethra plumicornis*. Another view is expressed by SALKIND, who has observed a swift appearance of stains in the cells of Malpighian tubes and alimentary canal of *Chironomus* (species not named) and a slow one in the same cells of *Corethra* (some larvae remained not stained after 6 days' swimming in 0.02 % neutralrot solution). SALKIND is of opinion that this difference is due to the cells of Malpighian tubes and intestine of *Chironomus* being hundred times as permeable as the corresponding cells of *Corethra* larvae.

To see if the distinctions in the staining of living larvae actually depends as SALKIND supposes, upon the properties of the cells of the organs in question I have tried to stain isolated organs. Alimentary canals dissected together with their Malpighian tubes from the bodies of the larvae of *Chironomus, Glyptotendipes* and *Corethra* were treated by 0.0001 % neutralrot diluted in Ringer's fluid. The appearance of first granules of stain takes place in the Malpighian tubes of *Glyptotendipes* after 4—6 minutes, in those of *Chironomus* and *Corethra* after 8—10 and 14—15 minutes respectively. Pericardial cells are stained still quicker. Consequently the cells of Malpighian tubes exhibit a very high efficiency as to the accumulation of stain granules from the solutions of very low concentrations; it should be emphasised that *Glyptotendipes* cells but not those of *Chironomus* show the quickest reaction, and thus evidently the distinctions in the staining of living larvae cannot be explained by the existence of respective differences in the premeability of these cells.

The above data also contradict to the SALKIND's assertion that neutralrot may penetrate into *Corethra* cells only at concentrations not below 0.01 %, which according to his opinion represents a threshold concentration indispensable to overcome the "Sperremechanismus" of the *Corethra* cells. It should be remarked here that from the necessity of a definite minimum threshold concentration for the appearance of the stain granules within the cells no conclusion may be drawn yet as to the existence of the special "Sperremechanismus" in the cell. The threshold concentration may by dependent not upon the phenomena of permeability but upon the formation of granules. In the case of the latter process not taking place the stain present in the cell may not be recognisable if the concentration in the surrounding solution is low (cf. GELLHORN 1929, p. 5). This is supported by the fact that when staining the isolated Malpighian tubes of *Corethra* coloured particles may be sometimes seen in the lumen before any traces of colour become conspicuous in the cells through which the stain has undoubtedly passed.

The above described distinctions in the staining of larvae may be explained only by the different speed

of neutralrot penetration into the larval body, the result of which is that a considerable concentration of stain is reached much sooner in the *Chironomus* haemolymph than in other larvae. This may be experimentally proved as follows: In *Glyptotendipes* larvae into aqueous 0.04 % solution of neutralrot at 16° C usually no granules at all may be discovered in the cells of Malpighian tubes for two days. Meanwhile in *Chironomus* larvae the formation of granules already begins after having kept them in the same solution for 2—4 hours. If to put the isolated intestine and Malpighian tubes of *Glyptotendipes* into a drop of haemolymph obtained from a *Chironomus* larva thoroughly washed and dissected after 25 hours of stay in neutralrot an undoubted appearance of the stain may be discovered in few minutes in the cells of *Glyptotendipes* organs. Consequently there is in the *Chironomus* haemolymph a concentration of stain that is sufficient to bring about a quick appearance of granules in *Glyptotendipes* cells, and thus the several days' absence of stain in *Glyptotendipes* larvae results from the slow appearance of the stain in their haemolymph.

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COMPARISON OF THE PENETRATION OF OTHER SUBSTANCES INTO THE LARVAE.

The assumption can be made that the slow penetration of vital stains into the body of *Glyptotendipes* and *Corethra* larvae is in correspondence with the low permeability of the latter by a number of other substances. If it is so, the indicated larvae should be more resistant against the action of poisons than those of *Chironomus*. This is supported by the FRANKENBERG's data (1915) who notices the stability of *Corethra* larvae against alcohol and their capacity to live in stagnant water. SALKIND has placed larvae into chloraeton solution and established that those of *Chironomus* become motionless in 10—15 minutes, while *Corethra* move normally for 3—5 hours.

I have studied the action of alcohol, acetic acid, ammoniac and corrosive sublimate on the larvae. The existence of the ability to move was tested by mechanical and light stimuli. The results of the experiments are totalled in the tables 1 and 2. The PAUSE's and SKADOVSKY's data (1924) that the movements stop first in the posterior segments of the body and then in the anterior ones are corroborated. Inspite of considerable individual variations which may depend upon a number of factors, the figures obtained lead to a quite definite conclusion: in all the experiments *Chironomus* larvae proved to be very sensitive to the studied poisons. As it may be seen in the tables the mobility of *Glyptotendipes* and *Corethra* lasts many dozens and sometimes several hundreds times as more as that of *Chironomus*. On comparing the resistance of *Glyptotendipes* to that of *Corethra* it should be pointed out

Table 1. *Mobility of larvae in diluted $HgCl_2$.*

% $HgCl_2$	5		2.5		1.0			0.2		0.1	
Species	Chir.	Gl.	Chir.	Gl.	Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.
Time of mobility in seconds	20	60	40	60	40	360	1 800	60	1 320	210	4 500
	25	90	45	100	40	480	2 400	135	1 620	240	4 800
	25	90	45	120	40	480	2 500	140	1 800	240	5 100
	30	90	50	150	50	540	2 500	150	2 100	240	5 200
	30	100	55	160	50	540	2 700	150	2 100	240	5 400
	30	100	60	180	50	540	3 000	165	2 220	300	5 400
	40	120	60	200	50	540	3 600	180	2 220	300	5 700
	50	120	60	240	55	660	3 600	240	2 220	360	5 700
	60	120	70	250	60	840	5 100	270	2 820	360	5 700
	90	180	120	260	120	960	6 000	330	3 240	360	6 000
Average time	50	107	60.5	172	55.5	594	3 320	182	2 166	285	5 350

Table 2. *Mobility of larvae in diluted ethyl alcohol, ammoniac and acetic acid.*

Solution	Ethyl alcohol 96 %		Ethyl alcohol 50 %			Ammoniac 10 %		Ammoniac 1.0 % ph 10.8			Acetic acid 5 % ph 2.3		
Species	Chir	Gl.	Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.	Cor.	Chir.	Gl.	Cor.
Time of mobility in seconds	<10	30	<10	1 080	1 800	10	55	30	480	1 200	<10	2 880	3 300
	<10	40	<10	1 080	1 860	15	80	30	540	1 320	10	3 000	3 600
	<10	40	10	1 200	1 860	20	90	30	600	1 800	15	3 900	4 200
	<10	40	10	1 200	1 980	25	90	30	600	1 800	20	4 500	4 500
	<10	45	15	1 500	2 100	40	100	35	720	1 980	20	4 500	5 400
	<10	50	15	1 800				40	780	1 980	30	4 500	6 300
	<10	50	25	1 860				40	900	2 520	30	5 400	7 800
	<10	60	30	1 980				60	960	2 700	30	6 600	7 800
	<10	75	30	2 100				90	1 020	2 880	40	6 900	10 800
	<10	80	55	3 000				150	1 260	3 600	50	7 200	14 400

that the results obtained may vary with the substances used. In 1 % sublimat and 1 % ammoniac the mobility of *Corethra* lasts about 10 times as more as that of *Glyptotendipes*. A much smaller difference is recorded in the 5 % acetic acid experiments while in 50 % alcohol *Corethra* and *Glyptotendipes* behave nearly alike. The difference in resistance of larvae becomes very outstanding when the water in the aquaria undergoes stagnation. On this occasion all the *Chironomus* larvae perish while those of *Corethra* swim normally and do not show any conspicuous reaction.

The described data show that the degree of the in-

clination of larvae to intravital staining and that of their sensibility to diluted poisons are in full correspondence with each other. On account of the period of the mobility of larvae in the solution of a given substance it is impossible, however, to conclude which are the quantitative distinctions between different larvae with regard to their permeability by the same substance or their sensibility to it. E.g. from the effect of 5 % corrosive sublimate solution the conclusion may be drawn that the resistance of *Glyptotendipes* larvae is 2.64 times as great as that of *Chironomus*. But another concentration results in other figures; the difference between the periods of mobility increases more and more if we pass on from high concentrations to low ones. The resistance of *Chironomus* in 1.0 % sublimate solution is 11.9 times and in 0.1 % 21 times as low as that of *Glyptotendipes*. Similarly 50 % alcohol and 1.0 % ammoniac disclose a greater difference of resistance between the two indicated larvae than 96° alcohol and 10 % ammoniac. When comparing by experiment how some two forms inhabiting chemically different waters resist a given substance it always born in mind that the figures obtained are relative and depend on the concentrations used. It is not unlikely that the equally low resistance of *Chironomus* and *Corethra* larvae against hydrogen sulphide described by NIKITINSKY and MUDREZOWA-WYSS (1930) depends upon the fact that the authors have raised the concentration of the gas in their experiments up to the saturation of its water solutions. Small differences in the permeability of larvae established in the laboratory conditions may become biologically important if in the natural environment there are poisonous substances in low concentrations. The difference of this sort may result in the survival of certain definite forms while those having a somewhat higher permeability may simultaneously perish.

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PENETRATION OF DILUTED SUBSTANCES THROUGH THE LARVAL INTEGUMENT.

To explain the fact of quick staining of *Chironomus* larvae and also their high sensibility to different poisons it is necessary to discover which is the way followed by the diluted substances during their penetration into the body cavity. During the first hours of staining (0.04 % solution) the granules of neutralrot appear in the exterior and interior fat-body, while no colour at all is yet seen in the intestinal epithelium. This fact suggests the idea of the penetration of stain through the integument. The assumption has been experimentally proved as follows. Fore and hind body ends of large *Chironomus* larvae are tied with thin strings and the larvae so placed over the stain solution that only the middle parts of their bodies are submerged both the mouth and

anal openings being raised totally above the surface of the liquid and the moistening of them rendered impossible. To retain the larvae still better in the described position a small load is often fixed to the middle part of the body with a little string. Several hours of keeping them in the 0.04 % neutral-rot solution suffice to obtain the accumulation of stain granules in the fat-body, mid-gut and Malpighian tubes.

Other substances have been tested by the same method. For example, if merging the middle part of the bow-like curved *Chironomus* larva into 1 % corrosive sublimate solution for one minute and even less, a complete loss of movements is the result. The dissection of the larvae thus treated shows that the cells of the alimentary canal and other organs are killed. Some 30 seconds of the action of 5 % acetic acid under the same conditions bring about the loss of the movements of larvae and gelatinisation of the protoplasm of the cells of intestine and Malpighian tubes.

The above result shows that the integument of *Chironomus* larvae is very permeable with regard to the studied substances and leads to the conclusion that the passage through the integument is the principal way of the penetration of these substances into the body cavity.

METHOD OF THE STUDY OF THE PERMEABILITY OF LARVAL CHITIN.

The passage of the chemical substances through the larval integument may depend either of the properties of the chitinous cuticle or on the permeability of the hypoderm. To elucidate the significance of the permeability of the chitinous cuticle and to compare the chitin permeability of different larvae I have evolved the following method. The first and the last body segments of the larva are cut off with the small sharp scalpel. The larval body thus operated is placed on a moist filtering paper sheet lying on a smooth piece of glass. Then the contents is squeezed out by rolling a round glass stick several times to and fro along the body. The remaining larval skin represents a minute chitinous tube opened at its both ends and totally deprived of hypodermal cell layer. I have convinced myself of the disappearance of the hypodermal layer by examining microscopical preparations made of the skins undergone the above mechanical treatment. The chitin cuticle is sufficiently strong to allow the application of considerable pressure during the squeezing out the viscera without the risk to break or damage the thin walls of the chitinous skin. There are no spiracles in the investigated larvae and no microscopical pores whatever in their chitinous

skins are present. Prepared skins are rinsed by water and besides this the end of a minute pipette is put under a binocular microscope in the opening of the skin and then the inside of the latter washed through by distilled water.

The permeability of the described chitinous tube for stains and poisons tested by means of the behaviour of the biological indicator—*Paramaecium*. After the described washing the culture of the latter should be somewhat concentrated with the aid of a centrifuge, taken with a pipette and then under a lens introduced into the lumen of the chitinous tube. The tube filled up with infusorians should be closed at its two ends by tying them with thin threads of surgical silk. Thus a sack is obtained that contains swimming infusorians, the latter being thus isolated by the chitinous membrane from the environment.[1] To make the described sacs of the chitinous skins of *Chironomus* and *Glyptotendipes* is not difficult at all; the work is somewhat more difficult in *Corethra* owing to the small size of its skins. The chitin of all the species investigated is sufficiently transparent and the infusorians placed within the sack may be examined both under the low and high magnifications of the microscope. Near the tightly tied thread the degree of permeability does not differ from that in any other place of the sack. The permeability of the chitin of different larvae may be studied comparatively by placing into a given solution the infusorians enclosed in the respective chitinous sacks and examining the resultant stoppage of movement or the appearance of colouration.

The above method is very suitable in a comparative study of the permeability of different chitins; but it is less so for the comparison of the penetration of different stuffs through a given chitinous membrane, because the distinctions obtained for the effects of some two substances may depend not only upon the differences in their penetrability, but also upon those in the sensibility of the infusorians with regard to the substances experimented with; this sort of interrelations being more difficult to analyse. Therefore to estimate the speeds of the penetration of different acids and alkalies through the chitin of given larvae I have filled up the skins with the chemical indicators. Nevertheless biological indicators may be of great service when it is impossible to discover by chemical method the presence of staining or toxic substances.

[1] The posterior segments of the body provided with gills are not used when preparing the above sacks and thus the question of the permeability of their chitin is left out of consideration in the present paper.

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PERMEABILITY OF ISOLATED CHITINOUS CUTICLE IN DIFFERENT LARVAE.

The observations and experiments dealt with in the foregoing show that the larvae of different species vary greatly as to the permeability of their integument. With the aid of the method described in the preceding paragraph it is possible to establish how far the indicated differences depend upon the properties of the chitinous cuticle. The results obtained are summarised in the tables 3 and 4. The figures show for how many seconds *Paramaecium* remain swimming within the chitinous skins, while in the case of neutralrot the time of the evident appearance of coloration in them is also given in seconds. Table 3 shows that neutralrot penetrates through the chitin of *Chironomus* much quicker than through that of *Glyptotendipes*; this results in an earlier staining of *Paramaecium* placed in a *Chironomus* chitinous skin. The coloration of *Paramaecium* placed in *Corethra* skins develops still slower; consequently the chitin of the latter larvae is still less penetrable for the stain. The results obtained fully correspond with the sequence observed in the appearance of the stain in the tissues of the larvae, of the latter are in the neutralrot solution. As it has been already indicated (cf. table 2) 50 % alcohol immobilizes the larvae of *Chironomus*

Table 3. *Staining of Paramaecium infusorians that are enclused in chitinous sacks placed in 1: 1 000 000 neutralrot solution.*

Treatment of chitin	Fresh chitin			Boiling in 20 % NaOH		Desincrustation in diaphanol		Boiling in water	
Species	Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.	Chir.	Gl.
Time of stain appearance in seconds	360	1 200	3 600	1 500	1 320	1 380	1 140	420	960
	360	1 260	3 900	1 740	1 680	1 620	1 920	600	1 020
	390	1 740	4 200	1 800	1 800	1 920	3 360	600	1 080
	420	1 800	6 300	1 860	1 800				
	480	1 800		2 160	2 100				
	540	1 980		2 160					
	600	2 100		2 280					
	600	2 940		2 360					
	660	3 300		2 700					
	720	3 720		3 060					
	780			3 300					

very soon, while the infusorians enclosed in its chitinous skin become immobilized in some 20—50 seconds. Meanwhile the infusorians protected from the influence of alcohol by the chitin of *Glyptotendipes* or *Corethra*

Table 4. *Time in seconds of the mobility of Paramaecium infusorians enclosed in chitinous sacks.*

Ethyl alcohol 50 %							Acetic acid 1 %						
Fresh chitin			Boiled in 20 % NaOH		Boiled in water		Fresh chitin			Boiled in 20 % NaOH		Boiled in water	
Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.	Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.
25	510	360	<10	<10	<10	70	20	780	360	<10	<10	<10	120
25	600	480	<10	20	20	85	20	900	360	<10	<10	15	120
35	600	480	<10	20	20	120	25	1 260	540	<10	<10	35	200
40	1 920	720					25	1 560	1 260				
50	2 040	2 040					30	2 100	1 500				

$HgCl_2$ 1 %							Ammoniac 1 %						
Fresh chitin			Boiled in 20 % NaOH		Boiled in water		Fresh chitin			Boiled in 20 % NaOH		Boiled in water	
Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.	Chir.	Gl.	Cor.	Chir.	Gl.	Chir.	Gl.
<10	50	240	<10	<10	<10	10	15	90	150	<10	<10	<10	
<10	70	420	<10	<10	<10	15	20	180	240	<10	<10	<10	
<10	150	480	<10	<10	<10	20	25	190	240	<10	<10	<10	
<10	170	660					35	210	250				
<10	200	960					60	240	300				

continue their swimming several dozen times longer. *Paramaecium* put in the chitinous cuticle of *Chironomus* and placed into 1 % corrosive sublimate solution perish in a few seconds, while the cuticle of *Corethra* may preserve their mobility in the same solution for 960 seconds. This result is in full accordance with the differences in the resistance of the indicated larvae to the action of corrosive sublimate. Experiments with the acetic acid and ammoniac have led to the same results.

Thus the experiments on skins show that chitinous cuticle represents the main factor upon which the degree of permeability of larval integument and the effect of diluted poisons and intra-vital stains are dependent. It is the low permeability of the chitinous layer of *Glyptotendipes* and *Corethra* larvae which renders them very resistant to poisons and deprives them of any considerable affinity to vital stains. It is out of doubt that besides the permeability of the chitin other factors may be also responsible for the stability of larvae: the permeability of hypoderm, increased permeability of gills (?), buffer condition of haemolymph and finally the resistance of the cells themselves whatever causes of this might be. All the enumerated factors influence the resistance of larvae to the action of

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diluted substances in a much lesser degree than the properties of the chitin.

EIDMANN (1922) has discovered that in *Periplaneta orientalis* the chitinous cuticle of the hind intestine is much better penetrated by KOH and HCl than that lining the crop. The author believes the indicated difference to be wholly due to the thickness of cuticle that being 5—8 μ in the crop and only 2 μ in the hind intestine. "... dünne Chitin-Membranen kein Hinderniss für osmotische Vorgänge zu sein brauchen, auch wenn sie keine Poren besitzen" (p. 432). But the differences of the degree of the permeability of skins can not be explained by these of the thickness of chitinous cuticle. The fact is that the chitin of *Glyptotendipes* is not thicker than or, but slightly surpasses that of *Chironomus*. But the chitin of *Corethra* larvae is very thin in spite of its minimum permeability. Its average thickness is about 1.5—3 μ while in *Chironomus* the chitinous layer reaches 7 μ and even more. STEUDEL (1913) has traced the penetration of iron salts through the very thick cuticle of hind intestine in *Melolontha vulgaris*. A study of the microstructure of the chitinous cuticle of larvae does not elucidate the causes of the differences of their permeability. We come to the conclusion that the chemical composition and physico-chemical properties of the cuticle are responsible for its greater or lesser permeability. Though a closer study of this problem is very difficult and lies out of the scope of the present paper, I have attempted nevertheless to establish whether the permeability of the cuticle typical of each species of larvae depends on the chitin itself or on the substances deposited in the chitinous cuticle — "Inkrusten" of the German authors. With the indicated view the skins deprived of hypoderm are boiled in the 20 % of NaOH and thoroughly washed through in several portions of distilled water. Then the skins are filled up with infusorian culture and placed in every of the solutions described in the foregoing. The chitin of *Chironomus* and *Glyptotendipes* has been studied by this method. While the two just mentioned species of larvae reveal very great differences in the permeability of their fresh chitin, the latter, if undergone "Desinkrustation" by NaOH, does not show any specific distinctions. The permeability of the skins of both species increases very much and alcohol, corrosive sublimate, acetic acid, ammoniac begin to pass with an equal speed through the chitin of *Chironomus* and *Glyptotendipes* (table 4). A somewhat lower permeability of *Chironomus* skins in some cases (alcohol) is possibly dependent upon the differences of the thickness of the chitin. The increase of the permeability of "desinkrustierten" chitin for alcohol, corrosive sublimate, acetic acid and ammoniac are contradicted by the experiments on the penetration of neutral-rot through it. The fact is that boiling in NaOH makes the chitinous skins of both species of larvae equally permeable, but instead of the increase of

permeability obtained for all the above enumerated substances neutralrot passes slower through the chitinous skin *Chironomus* larvae after "Desinkrustation" than before it; meanwhile the permeability of *Glyptotendipes* skins remains almost unchanged (table 3). This particular behaviour of neutralrot seemed to me not verisimilar and therefore the above experiment was many times repeated. To avoid the immediate action of the NaOH remains on the coloration they are eliminated from the skins by 3—4 days' washing, and subsequently the skins are neutralised by acid. But inspite of this an evident slowing down of the neutralrot penetration through the "desinkrustierte" *Chironomus* skins has been obtained in all the experiments. Quite similar results with regard to neutralrot are obtained if using diaphanol for "Desinkrustation" (table 3). Meanwhile all the other substances (alcohol, acetic acid, corrosive sublimate) begin to penetrate quicker than through the fresh chitin like it is the case after the NaOH treatment. But an attempt to obtain equal penetrability of *Chironomus* and *Glyptotendipes* skins for alcohol and corrosive sublimate by keeping them in diaphanol for three days proved to be unsuccessful. Boiling in water alters but slightly the penetration of neutralrot (table 3); the speed of the penetration of other substances becomes higher, but the difference in the permeability of *Chironomus* and *Glyptotendipes* still remains considerable (table 4).

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The fact does not stand alone that a certain treatment of the cuticle (boiling in NaOH) raises very much its permeability for a number substances and lowers it for some others (neutralrot) if borning in mind the data given in GELLHORN's work (1929). It is rather difficult to comprehend what may be the essence of this influence upon the membrane. Having no facts to solve this problem, the following hypothetical explanation may be offered. Under the NaOH or diaphanal treatment the "Inkrusten" most likely hindering the penetration of the cuticle by other chemical compounds are eliminated; if on the other hand the treatment alters the chemico-physical properties of the chitin and makes its pores narrower the increase of the permeability for molecular solutions and the decrease of that for colloidal particles of neutralrot should be the result. Whether this hypothesis is true or not, the described data show that the "Inkrusten" are very important for the estimation of the permeability of chitinous cuticle.

PERMEABITILY OF CHITIN FOR ACIDS AND ALKALIES.

Among the variety of the ecological factors influencing aquatic organisms that of pH ions concentration is one of the most interesting to study. The important significance of the pH environment is shown in the series of papers by SKADOVSKY and his collaborators (1928). In the natural conditions the

reaction of the environment may fluctuate within a very wide range. Among the fresh water basins there are, for example, distrophe sphagnum ponds in which pH may be below 4, and also some eutrophe basins which show pH above 10. The concentration of hydrogen ions is liable to very great changes of seasonal character even within the limits of a given basin. In one of SKADOVSKY's papers (1924) the behaviour of *Chironomus* larvae in different pH is studied. In the solutions of HCl at pH = 3, and more, the larval movements remain normal during 4—5 days; they also prove to be but slightly influenced by KOH. On this account SKADOVSKY considers the larvae of plumosus group of *Chironomus* as one of "euryhydrogenione" that may sustain fluctuations in the concentration of hydrogen ions ranging far beyond these occurring in natural conditions. In the same paper a higher toxicity of the acetic acid and ammoniac is noticed by SKADOVSKY as compared to HCl and KOH. But the toxic action of the two former substances is independent from the change of the concentration of the hydrogen ions produced by them being due, according to the SKADOVSKY's view, to the activity of the not dissociated molecules. "The action of the acetic acid is not a typical example of that of acids in general sience in the present case the active rôle is played no by $H^{\cdot}$ but by the non-dissociated CH_3COOH molecules owing to their capillar activity" (l. c. p. 10).

The facts established by SKADOVSKY are wholly corroborated by my own observations on *Chironomus plumosus*. The larvae of the latter placed in the acetic acid at pH 2.3 become immobilised on the average after 30 seconds; 110 seconds are necessary to stop the larvae at pH 3.35 in the same acid (averaged from 12 observations). But in the HCl solution at pH 2.3 the larvae live and move normally for a great number of days. A not less striking contrast is obtained from the comparison of the effect of NaOH to that of ammoniac. If to raise pH to 10.8 by NaOH the larvae live in such a medium for days. But if the same concentration of hydrogene ions is brought about by ammoniac, the larvae become immobilised after 90 seconds (averaged from 10 observations).

There is a very great number of examples in literature which show that the strongly dissociated acids and alkalies slowly penetrate through the selectively-permeable animal and plant membranes while the latter are quickly penetrated by the feebly dissociated acids and alkalies. Acetic acid and ammoniac just belong, as it is known, to the latter category, and their quick penetration is proved in many different organisms. It is natural to assume that the chitinous cuticle is governed by similar regularities. To ascertain if the chitin represents a selective permeable membrane I have turned again to the experiments on the isolated cuticles of *Chironomus* larvae. The penetration of HCl and NaOH on the one hand and that of acetic acid and ammoniac on the other have been compared; in these experiments, however, owing to

the cause already noticed the chemical indicator has been used instead of the biological one. To study the effects of HCl and acetic acid the skins are filled up with the solution of bromphenolblau which, if within the limits pH 6—3.0 converts blue colour into yellow. In the skins merged into acetic acid at pH 2.3 the indicator begins to grow yellow after a few seconds, and in 30 seconds the process is completed. If the skins are placed in HCl at the same pH the change of the hue of the indicator begins only after some 20 minutes. Still a greater difference has been obtained in the comparison of the penetration of ammoniac and NaOH the concentration of hydrogen ions being 10.8 in both cases. Thymolblau has been used as indicator which turns from yellow into blue at the pH transition from 8.0 to 9.6. If the *Chironomus* skins containing thymolblau are placed in the ammoniac solution (pH 10.8) the indicator becomes quite blue after 20 seconds. In the NaOH solution (at the same pH) the blue coloration of the indicator may be completed only on the expiration of several hours; some skins exhibit yellow or olivaceous hue of the enclosed indicator still on the next day. In all the experiments NaOH was many times replaced by fresh portions and measures were taken to preserve it from the neutralising action of the atmospheric CO_2. If a skin lying in ammoniac and containing blue indicator is placed into NaOH solution, the indicator acquires very soon a more sour character and becomes olive-yellow. In this case the easily penetrating ammoniac leaves the skin quickly but is not compensated by NaOH owing to the latter's property of penetration being extremely low.

On the basis of the above experiments it is possible to explain the differences in the action of the acids and alkalies on the larva by the different rates of their penetration through the chitinous cuticle. Owing to this the acetic acid and ammoniac alter very soon pH of tissues and haemolymph and cause the death of larvae. The influence of HCl and NaOH on the ionic hydrogen concentration of the larval body protected by chitinous cuticle is much less considerable. The selective permeability discovered in fresh chitin disappears totally after the skin is "desinkrustiert" either by boiling in NaOH or by action of diaphanol. HCl and NaOH penetrate "desinkrustierten" chitin very quick.

The obtained results show once more that the kernel of the problem lies not in the influence of a given concentration of hydrogen ions on the organism in general, but in that of different concentrations of certain acids and alkalies. The final effect more depends upon the substances by which the existing reaction of the environment is brought about, than on the absolute pH value. After PAUSE the resistance of the larvae of *Chironomus gregarius* to the acids is but insignificant; this conclusion is undoubtedly due to the fact that he has experimented with the acetic acid and

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KOH the latter being a slowly penetrating alkali. Hence the experimentally etablished concepts of "euryhydrogenionität" and "stenohydrogenionität" may be only of relative value. It should be more correct when working in ecology by laboratory methods to investigate the influence of pH by producing it by the same substances which are responsible for the acid-alkaline equilibrium of water in the natural conditions.

AGE AND SEASON CHANGES OF PERMEABILITY.

The data on the chitin permeability described in the foregoing text may be supplemented by the influence of age and season on it, met with during my studies. The respective facts are dealt with but briefly as no special investigation into the problem has been carried through. Very clear changes of permeability dependent upon the age have been discovered in the larvae of *Chironomus plumosus*. Both the experiments on the skins and the study of the action of substances on the living larvae reveal a much greater permeability in young specimens than in the two last larval instars. The latter were used as principal *Chironomus* material for the present work.

The attemps to find out the age differences in the larvae of *Glyptotendipes* were unsuccessful: *Glyptotendipes* larvae of 5 mm. length are as resistant to the action of poisons as those taken just before pupation. All the data on the permeability of *Corethra* larvae given in the foregoing are obtained from those catched in September and October of 1932 and 1933. The larvae catched in the same pond in spring and summer months have shown a much greater permeability. The future study of seasonal and age changes of permeability may lead to a number of ecologically interesting conclusions.

PENETRATION OF DILUTED SUBSTANCES THROUGH THE ALIMENTARY CANAL OF LARVAE.

According to my investigations the larvae of *Glyptotendipes* and *Corethra* may remain alive for long periods in different diluted poisons owing to the low permeability of their chitin. The latter peculiarity is also responsible for their remaining unstained if placed for long in the solution of Neutralrot. The very fact that the larvae is protected by its slightly permeable chitinous integument from diluted substances suggests the idea that the penetration of the latter into the haemolymph through the alimentary canal is also very limited. The latter circumstance may be due either to the low permeability of the intestinal walls for the studied substances or generally to the fact that the volume of the surrounding liquid passing into the intestinal cavity

is but small. To decide which of the two alternative causes hinders the penetration of poisons and stains through the alimentary canal we have to find out if the wall of the intestine is penetrable. In KOLMER's work (1904) a very good proof of the penetration of methylene blue is given. The author kept larvae for weeks in concentrated solutions of methylene blue and did not obtain any coloration; the latter, however, appeared very soon after having fed the larvae with stained *Stentor coeruleus*. To elucidate the penetration of neutralrot through the intestinal wall I have experimented as follows. A narrow glass pipette is filled up with 0.04 % neutralrot solution. Under the binocular microscope the end of the pipette is pushed into the mouth opening and the stain squeezed out. Being pressed by the pipette the stain fills up the muscular pharynx, passes through the narrow oesophagus into the mid-gut and stains the contents of its cavity. Of course one has to avoid running the pipette through the walls of the mouth cavity and pharynx which technique is, however, not difficult. In a few minutes after the described artificial injection of the stain, the granules of neutralrot may be seen that have appeared abundantly in the epithelium of the mid. intestine. The larvae injected with the stain are placed into a vessel of distilled water. In about 20 minutes a marked coloration appears in the pericardial cells; and the emphasis should be laid on the fact that principally those of the pericardial cells are stained which lie near by the stained portion of the intestinal epithelium. Then, if the injection takes place but once, the pericardial and intestinal cells gradually lose their stain and the latter comes to concentrate in the larval integument (the latter circumstance is wholly in accordance with NAGEL's data). The above experiments show that the intestinal walls of *Corethra* are highly permeable, and that the stain when put into the intestinal cavity is very soon transferred to the haemolymph and located in different cells of the larva. If the injected stain remains in the muscular pharynx and does not reach the mid-gut, no coloration of larval cells takes place. Consequently like the chitin of the integument that lining the whole of the fore intestine of the larvae (including pharynx) is but slightly permeable. The injection of corrosive sublimate and acetic acid solutions results in the intestinal walls becoming instantly turbid and their cells fixed. *Glyptotendipes* larvae show no coloration after staying for many hours in the 0.04 % neutralrot solution. But be the latter injected in their intestine the coloration appears instantly. The absence of stain in the cells of the larvae of *Corethra* swimming several days in the neutralrot solution and the very slow staining of *Glyptotendipes* larvae may be explained only by the fact that these larvae do not swallow the solution surrounding them. The descriptions of the

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feeding mechanism of the larvae of *Corethra* (LEYDIG 1851, WEISSMANN 1866) show clearly that when they swallow their food no considerable amount of surrounding water should pass into their mid-gut. It is likely that the larvae of *Glyptotendipes* and *Chironomus* also swallow almost solely solid particles. To quite similar conclusions came WIGGLESWORTH (1933) who discovered that the larvae of *Aedes argenteus* if placed into suspension of trypane blue swallowed the particles of stain without any considerable quantity of water. The author concludes that "normally the larva swallows very little fluid" (l. c. p. 25). On account of the above said the SCHNEIDER's data (1904) on the current of fluid through the alimentary canal of Chironomids and its supposed respiratory significance should be regarded as based on evidently erroneous observations.

A further detailed study of the permeability of chitinous integument in different forms deserves serious attention from several points of view. If the penetration of diluted substances through the alimentary canal is but unimportant the decisive role in the penetration or non-penetration of these substances in the larval body should be evidently played by the selective permeability of the chitinous cuticle. If so the investigation into the permeability of the latter in aquatic organisms becomes of great importance for their ecology. From the ecological point of view it is very interesting, for example, to study the permeability of the typical inhabitants of distrophe waters and to compare them systematically to the organisms living in the waters which contain substances of physiologically more indifferent character. To elucidate the adaptive importance of the different degrees of the chitin permeability of different larvae one has to compare it with the permeability of egg-cells in the same species. The problem of the penetration of water through the chitin is of profound physiological interest with regard to the elucidation of the mechanism of osmoregulation in the aquatic arthropods that is scarcely studied yet (see WIGGLESWORTH 1933). Finally from the practical point of view the investigation of the permeability of chitinous integument may prove to be valuable in the work of improving the methods of the use of contact insecticides.

CONCLUSIONS.

1. The investigation of the larvae of *Chironomus plumosus, Glyptotendipes polytomus* and *Corethra plumicornis* has shown in them great differences as to the vital coloration by the solutions of basic stains on the one hand and the resistance to the influence of the solutions of corrosive sublimate, ethyl alcohol, acetic acid and ammoniac on the other.

2. The larvae of *Chironomus plumosus* show the maximum inclination to staining and sensibility to poisons. In *Glyptotendipes* larvae the indicated properties are much less pronounced, in *Corethra* they are at the minimum.

3. The differences between the larvae in their relation to diluted substances are dependent upon the rate of the penetration of the latter into the body cavity of the larvae.

4. Owing to the extremely restricted penetration of the surrounding fluid into the cavity of larval intestine the action of the substances diluted in it is determined by their permeating through the larval integument.

5. A method is evolved by which the chitinous cuticle of the integument is mechanically isolated and *Paramaecium* infusorians used as indicators. It allows to study the permeability of chitin immediately.

6. The work by this method shows that the permeability of the integument is essentially due to the permeability of its chitinous cuticle.

7. A comparative study of cuticle in the three species of larvae has shown a high permeability of the cuticle in *Chironomus*, a very low permeability in *Glyptotendipes* and a still lower in *Corethra* larvae.

8. The above specific distinctions are independent from the variation in the thickness of chitinous cuticle, and are most likely due to differences of chemical and physico-chemical properties of the cuticle.

9. The chitinous cuticle represents a selective permeable membrane, and being easily penetrated by acetic acid and ammoniac is hardly penetrated to strong acids and alkalies.

10. A given concentration of hydrogen ions may lead to quite different effects; this depends upon whether the substances having brought it about penetrate easily or with difficulty through the chitinous cuticle.

11. The substances which are deposited in the chitin—"Inkrusten"—play a most important role in its permeability. "Desinkrustierte" chitin shows neither specific differences nor selective properties in its permeability.

12. "Desinkrustation" of the chitin markedly rises its permeability for alcohol, corrosive sublimate, acetic acid, ammoniac, but the permeability of the "desinkrustierten" chitin of *Chironomus* becomes considerably lower for neutralrot.

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CONTRIBUTIONS A L'ÉTUDE DE L'AUTOFÉCONDATION CHEZ LES OLIGOCHÈTES

PAR

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(Avec 2 planches et 8 figures dans le texte)

I. INTRODUCTION.

Conformément au principe de causalité nous ne pouvons pas interpréter la protérandrie (respectivement la protérogynie) comme un phénomène d'adaptation dont le but est d'éviter l'autofécondation. Nous ne puovons que constater le fait que dans des cas très nombreux l'autofécondation n'a pas lieu grâce à l'existence du phénomène en question ainsi qu'au fait que chez les animaux hermaphrodites la libido d'un individu est ordinairement dirigé sur un autre. D'après W. WHEELER (1896) et E. MAUPAS la protérandrie dit être interprétée seulement comme un résultat de l'évolution physiologique des produits génitaux, les spermatozoïdes ayant presque toujours un développement plus précoce que les œufs. Quoique dans plusieurs cas on soit en présence de facteurs rendant impossible la fécondation directe ou, même, en présence de l'incapacité de la pénétration du spermatozoïde dans l'ovule du même individu, et quoiqu'on connaisse dans d'autres cas l'effet négatif de l'autofécondation, on n'est pourtant pas autorisé à tenir l'autofécondation pour un processus qui «im grossen und ganzen ungünstig wirkt» (O. HERTWIG, 1920, p. 388) ou pour un phénomène contre lequel il existe dans la nature une certaine tendance négative. On doit adopter l'opinion de E. MAUPAS (l. c.) d'après laquelle le croisement et l'autofécondation «ne sont en somme que des adaptations particulières de la reproduction ovogénétique et, comme toutes les adaptations biologiques sont sujettés à varier. Que le mode par croisement soit le plus répandu, qu'il jouisse même de propriétés speciales, c'est ce qui semble bien résulter de l'état actuel de nos connaissances. Mais il n'exclut pas pour cela d'une façon absolue le mode plus primitif et plus simple de l'autofécondation. L'un et l'autre coexistent parallèlement et sont nécessaire ou different suivant les cas» (p. 611).

CONSTANTIN GAVRILOV

L'étude détaillée de l'autofécondation chez les animaux hermaphrodites[1] nous montre que dans plusieurs cas ce processus est une modalité permanente de reproduction et qu'il peut, à titre de phénomène secondaire, remplacer définitivement la fécondation croisée. Dans d'autres cas il peut exister à titre de modalité supplémentaire à côté de l'accouplement réciproque. Il contribuerait dans les cas en question à la conservation de l'espèce dans les conditions rendant la copulation normale impossible.

C'est de ce dernier point de vue que le problème d'autofécondation chez les Oligochètes doit nous intéresser.

En 1928 M^r^ le D^r^ ČERNOSVITOV m'avait donné l'idée d'entreprendre des recherches systématiques sur ce sujet. Poursuivies depuis ce temps (avec une année d'interruption) ces recherches ont donné les résultats que j'expose dans le présent mémoire. Ils sont loin de donner la solution définitive du problème, plusieurs questions restant ouvertes. Je ne les considère qu'en qualité de matériel, pouvant servir de point de départ pour des recherches ultérieures. Quelques-unes de mes expériences ne servent qu'à l'orientation préliminiaire.

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Le présent travail est surtout consacré à l'étude des questions suivantes:

1) La faculté de se reproduire sans fécondation croisée, constatée par L. ČERNOSVITOV (1927) chez *Tubifex tubifex* MÜLL., est-elle propre exclusivement à cette espèce ou existe-elle aussi chez d'autres Oligochètes?

2) Peut-on expliquer cette particularité, comme le fait L. ČERNOSVITOV, par l'autofécondation, ou sommes-nous en présence de cas de parthénogénèse?

3) En cas d'autofécondation comment ce processus, s'effectuet-il, autrement dit, quel est son mécanisme?

Je dédie ce travail à la mémoire de mes chers Maîtres, M^r^ le Prof. D^r^ J. WENIG et M^r^ le Doc. D^r^ J. HAHN dont la mort prématurée a profondement ému tous ceux qui ont eu le bonheur de les connaître. Les précieux conseils qu'ils ne cessaient de me prodiguer et le vif intérêt qu'ils manifestaient toujours pour mon travail m'ont apporté une aide précieuse au cours de mes recherches.

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[1] Un court aperçu de l'autofécondation chez les Métazoaires hermaphrodites fait le sujet d'un autre travail.

Mes remerciements vont aussi à la fondation «Université de Moscou», organisée par l'Université Populaire Russe à Prague, qui m'a donné la possibilité d'achever mon travail.

II. APERÇU DE LA LITTÉRATURE.

Les renseignements concernant l'autofécondation chez les Oligochètes, que nous trouvons dans la littérature sont très peu nombreux. On peut dire que jusqu'à présent ce problème n'attirait pas l'attention des chercheurs, bien que la première indication sur la possibilité du phénomène en question eût été faite il y a plus de 30 ans.

Nous la trouvons dans le travail de A. Štolc (1901, v. aussi 1902) consacré à l'étude du cycle évolutif des Annelés inférieurs d'eau douce. A. Štolc a signalé chez *Aeolosoma quaternarium* Ehrbg. des pontes non précédées de copulation croisée. Les deux exemplaires de cette espèce, que cet auteur avait isolés, ont pondu seulement trois œufs. Leur sort ultérieur étant resté inconnu à l'auteur il faut considérer sa supposition concernant l'autofécondation comme insuffisement basée et demandant une vérification ultérieure.

L. Černosvitov (1927) a abordé de nouveau le problème de l'autofécondation chez les Oligochètes sans prendre en considération le cas cité ci-dessus. Ce furent les phénomènes observés par cet auteur chez *Tubifex tubifex* Müll. qui lui donnèrent l'idée d'entreprendre l'étude du problème en question. L. Černosvitov a trouvé des exemplaires de *Tubifex tubifex* dont les spermathèques n'étaient développées que d'un côté ou même faisaient entièrement défaut, tandis que toutes les autres parties de l'appareil génital restaient tout à fait normales. L'auteur est porté à envisager ce phénomène comme une anomalie. En tout cas il n'est pas dû à la régénération de la partie antérieure du corps. L'étude de la régression physiologique de l'appareil génital de *Tubifex* après la fin de la période d'activité sexuelle (L. Černosvitov, 1930 a) montre que ces cas ne peuvent pas être expliqués par une régression précoce des spermathèques qui précèderait celle des autres parties de l'appareil génital, les deux réceptacles dégénérant toujours simultanément. D'un autre côté, à l'époque où commence leur régression, les autres parties de l'appareil génital présentent déjà certains symptômes de dégénérescence.

L'anomalie n'est propre à aucune localité définie. L. Černosvitov l'avait constatée dans différents endroits de Tchécoslovaquie. Plus tard (1930) il en parle dans son travail sur la faune oligochétique de la Bosnie. Le pourcentage d'exemplaires anormaux est très différent. D'après le tableau donné par L. Černosvitov (1927) il varie entre 1,7 et 58,3 tout en restant plus bas dans les localités où *Tubifex* se rencontre en grandes masses et présente des dimensions considérables. Au contraire dans des localités, où

cette espèce est présentée par un nombre restreint de petits exemplaires, le pourcentage d'individus anormaux devient considérable.[1] Ce phénomène oblige L. ČERNOSVITOV à chercher la corrélation entre le degré de développement des spermathèques chez le *Tubifex* et les conditions d'alimentation.

L'absence des deux réceptacles rend impossible la fécondation réciproque. L. ČERNOSVITOV établit pourtant que les œufs dans les cocons pondus par des exemplaires présentant l'anomalie en question, sont capables de se développer tout à fait normalement. De plus, cet auteur avait signalé la même faculté chez les œufs des exemplaires normaux de *Tubifex* isolés, dont les spermathèques ne présentaient pas de spermatophores. En outre il a observé le développement des œufs éliminés par les individus isolés encore bien avant leur maturité sexuelle, toute possibilité d'accouplement ayant été ainsi exclue.

Le pourcentage d'œufs, qui ne se développaient pas au cours de chacune des trois série d'expériences citées ci-dessus, était faible.

Selon L. ČERNOSVITOV la faculté des œufs de se développer sans être fécondés par le sperme d'un autre individu peut être interprêtée de double façon: ou comme l'autofécondation ou comme la parthénogénèse.

L'auteur espérait obtenir la solution du problème en étudiant les processus d'expulsion des globules polaires chez le *Tubifex*. Se basant sur les résultats de ses recherches concernant les œufs fertilisés par le sperme d'un autre individu ainsi que les œufs se développant sans la fécondation croisée, l'auteur est porté à envisager la première supposition (autofécondation) comme la plus vraisemblable. J'aurai encore l'occasion de revenir sur ces résultats de

Tableau I.

Localité	Date d'observation	Nombre total de vers étudiés	Individus asexués	Individus à l'appareil génital en voie de régression	Individus à l'appareil génital normal	Avec 1 rec. sem	Sans rec. sem
Újezd nad Lesy . (étang)	XI et XII 1928; III, IV, VI, XI, XII 1929; V 1930; XI et XII 1931	252	32	9	114 (45,2 %)	15 (5,9%)	82 (32,5%)
Běchovice . . . (mare)	IV 1929	12	1	—	10 (83,3 %)	1 (8,3%)	—
Mokropsý, fleuve Berounka . . .	X, XI 1929	11	5	3	2 (18,1 %)	—	1 (39 %)
Total		275	38	12	126 (45,8 %)	16 (5,8%)	83 (30,1%)

[1] Au cours de mes expériences j'ai souvent procédé à l'établissement du nombre d'individus anormaux de *Tubifex tubifex* provenant de différentes localités et je ne peux que confirmer l'opinion de L. ČERNOSVITOV sur la fréquence de ce phénomène. Le tableau I donne les résultats de mes observations.

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L. ČERNOSVITOV, quand je traiterai ceux de mes propres recherches sur *Limnodrilus hoffmeisteri.*

J'aurai aussi besoin de répéter ci-dessous les suppositions de L. ČERNOSVITOV concernant le mode d'autofécondation chez *Tubifex tubifex.* Cet auteur admet deux modalités possibles du processus d'autofécondation: 1) ou les spermatozoïdes pénètrent dans le cocon au moment de la ponte, après avoir parcouru les conduits déférents, 2) ou ils fertilisent les ovules encore dans le corps du ver, pénétrant des sacs spermathiques dans les ovisacs. Il n'y a pas donc d'autocopulation. Déjà la position des orifices génitaux mâles et celle des orifices des spermathèques la rendent impossible.

Nous ne trouvons pas dans la littérature d'autres indications directes sur l'existence d'autofécondation chez les Oligochètes.

Comme je l'ai déjà indiqué dans mon travail préliminaire (1931) L. ČERNOSVITOV a établi que les œufs de l'*Enchytraeus albidus* HENLE, eux aussi, sont capables de se développer sans être fécondés par le sperme d'un autre individu. Ces résultats de caractère préliminaire que l'auteur, lui-même, n'avait pas encore publiés, sont basés sur un matériel peu nombreux. Il faut aussi noter que seuls les premiers stades de segmentation ont été observés. Ce qui reste inconnu c'est si les œufs étaient capables d'achever leur développement. L'autocopulation, dont la possibilité théorique ne paraissait pas exclue chez cette espèce, n'a pas été signalée.

Les résultats des expériences de Mr le Prof. Dr V. JANDA avec *Rhynchelmis limosella* HOFFM. et avec *Criodrilus lacuum* HOFFM. qui restent également inédits[1] sont aussi basés sur un matériel peu nombreux. Ces résultats ont été négatifs. Le pourcentage des vers à l'appareil génital, développé après l'isolation, qui pondaient des cocons était très insignifiant. Les œufs qu'ils renfermaient ne se développaient pas.

III. MATÉRIEL ET TECHNIQUE.

Le tableau II, p. 26 donne la liste d'Oligochètes, dont les réprésentants m'ont servi de matériel au cours de mes recherches.

Le strict isolement des individus rendant impossible la fécondation croisée était la condition essentielle des expériences. Les vers ont été isolés toujours avant le commencement de la période d'activité sexuelle.

Limnodrilus. — J'isolais les exemplaires dont les segments génitaux ne présentaient que de petites ébauches sacciformes de gonades situés des deux côtés de l'intestin. Plus rarement c'étaient des individus aux stades plus avan-

[1] C'est un agréable devoir pour moi de remercier ici Mr le Prof. Dr V. JANDA pour son aimable permission de les publier.

Tableau II.

	Famille, genre, espèce	Localité	Date d'expérience
	Fam. TUBIFICIDAE		
1.	*Limnodrilus udekemianus* CLAP.	Újezd nad Lesy (étang) Strašnice (étang)	Avril, mai 1929. Décembre 1930. Octobre 1931.
2.	*Limnodrilus hoffmeisteri* CLAP.	Újezd n. L. (étang) Běchovice (mare) Mokropsý (fl. Berounka)	Avril, mai, novembre, décembre 1929. Octobre, novembre 1931.
3.	*Limnodrilus claparedeianus* RATZEL	Mokropsý (fl. Berounka) Běchovice (mare)	Avril, octobre 1929.
	Fam. LUMBRICULIDAE		
4.	*Rhynchelmis limosella* HOFFM.	Čelakovice (fossés)	Novembre 1931.
	Fam. LUMBRICIDAE		
5.	*Eiseniella tetraedra forma typica* (SAV.)	Šárka (mare)	Octobre 1931.

cés chez lesquels on observait déjà les ébauches des sacs séminaux en voie de formation, tandis que les spermathèques n'étaient pas encore développées.[1]

Malgré le grand nombre d'individus examinés, je n'ai jamais observé chez ce genre, l'absence complète ou unilatérale des réceptacles séminaux, tandis que ce phénomène était, comme nous l'avons vu, très commun chez l'espèce voisine — *Tubifex tubifex*.

Quant à la présence des spermatophores dans les spermathèques on ne peut la constater avec certitude d'après les exemplaires vivants que chez *Limnodrilus udekemianus*. Il est au contraire extrêmement difficile de se prononcer sur ce sujet quand on est en présence des ampoules insuffisemment transparentes de *L. hoffmeisteri* ou de *L. claparedeianus*. A cause de celà il était impossible de procéder à l'isolement des individus sexuellement mûrs mais ne présentant pas de spermatophores dans les réceptacles (L. ČERNOSVITOV a entrepris une série d'expériences de ce genre avec *Tubifex tubifex*).

Rhynchelmis. — J'isolais ou des exemplaires complètement asexués ou ceux, chez lesquels les ovules, renfermés dans les ovisacs, se faisaient voir à travers les parois du corps comme des taches blanches, mais le clitellum différencié faisait encore défaut.

Eiseniella. — On isolait des exemplaires encore très petits et immatures.

Chaque individu isolé a été placé dans un récipient de verre ou d'argile de grandeur suffisante avec une certaine quantité d'eau et du substratum spécialement préparé.

[1] Dans mon travail préliminaire j'ai indiqué qu'à ce stade les ovisacs commencent aussi à se developper. En réalité leur développement s'effectue plus tard.

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La préparation du substratum devait se faire très soigneusement. Je me servais ordinairement de la vase, prise du bassin, installé dans la cour de notre Institut de Zoologie, plus rarement de la vase prise dans les localités d'où provenaient les vers. Cette vase soigneusement triturée dans un mortier de porcelaine était ensuite examinée par petites portions dans des boîtes de Petri.[1] Surtout le detritus destiné à l'élevage de *Limnodrilus* a dû être très menu ce qui facilitait beaucoup à trouver les petits cocons de ce genre couverts de grains de sable. Quant à *Rhynchelmis* et à *Eiseniella,* la vase dans laquelle ils étaient élevés, a été mélangée avec des feuilles, provenant des habitats de ces vers. Ces feuilles étaient préalablement soumises à un contrôle minutieux afin d'en enlever tous les animaux.

Les trois espèces de *Limnodrilus* avec lesquelles j'ai expérimenté atteignaient la maturité sexuelle dans l'eau de robinet aussi bien que placées dans l'eau prise du bassin de notre Institut. Au cours de mes expériences avec *Rhynchelmis* et *Eiseniella* je n'ai employé que cette dernière.

Les élevages de *Limnodrilus* et d'*Eiseniella* ont été entretenus à la température de laboratoire (plus de + 20°), celles de *Rhynchelmis* à la température qui oscillait entre + 5° et + 10° C.

De temps en temps les individus ont été soumis au contrôle (surtout souvent pendant la période de ponte). Le substratum a été examiné dans des boîtes de Petri. Les cocons pondus ont été placés dans des récipients spéciaux avec de l'eau pure. Le nombre initial d'œufs dans les cocons de *Limnodrilus* étant difficile à établir grâce aux particules de vase qui les entouraient, j'ouvrais ordinairement les cocons quelque temps après la ponte pour pouvoir compter les œufs en voie de développement.

Chaque individu qui avait pondu un certain nombre de cocons était ensuite fixé (le plus souvent avec le Zenker) ce qui me permettait d'étudier sur les coupes (coloration avec l'Hämalaun, le Heidenhain ou avec Delafield — éosine) le contenu des réceptacles séminaux.

Pour étudier du point de vue cytologique les processus d'expulsion des globules polaires dans les œufs de *Limnodrilus hoffmeisteri* — fertilisés et non fertilisés par le sperme d'un autre individu, j'ai entrepris deux séries parallèles d'expériences:

1) On isolait les vers avant qu'ils aient atteint la maturité sexuelle.

2) On plaçait les vers après la copulation (c'est-à-dire ceux, dont les spermathèques présentaient des spermatophores b i e n v i s i b l e s) dans un récipient commun avec de la vase triturée, de sorte que les accoupplements reitérés n'étaient pas impossibles.

[1] La meilleure méthode de contrôle supplémentaire du substratum préparé est la suivante: on répartit la vase triturée par petites portions dans des recipients et on les laisse pendant quelques jours en repos. Si un ver avait par hasard persisté on voit ensuite nettement ses tracés.

Chaque exemplaire isolé, ainsi que le récipient commun étaient soumis au contrôle deux fois par jour. Les cocons trouvés dans le substratum, débarassés autant que possible des particules de vase et des grains de sable à l'aide de petits pinceaux (sous la loupe binoculaire) et prudemment perforés, étaient ensuite fixés avec le Zenker pendant $^3/_4$—1 heure. Après un court lavage (1—2 heures) je les transportais dans l'alcool à 70 %. L'inclusion à la paraffine s'effectuait comme suit:

Alcool à 95 %	20—30 minutes
Alcool absolu	20—25 min.
2 volumes d'alcool abs. + 1 vol. de xylène	20—30 min.
1 volume d'alcool abs. + 2 vol. de xylène	20—30 min.
Xylène pure	20—30 min.
Xylène + paraffine	25—30 min.
42° paraffine	1 heure
52° „	1 heure
56° „	1—1 $^1/_2$ heures

Dans certains cas je fixais séparément les œufs débarassés de la gaine de cocon (pendant 15—20 minutes). L'inclusion à la paraffine s'effectuait après la coloration préalable avec l'éosine. Les œufs ne restaient dans chacun des liquides mentionnés ci-dessus que pendant 15—20 minutes. Cette méthode de fixation est pourtant moins commode car les globules polaires se détachent souvent des œufs et se perdent.

Les coupes épaisses de 7 μ, plus rarement de 10 μ, ont été colorées avec l'haematoxyline ferrique de Heidenhain — l'éosine.

IV. RÉSULTATS.

A. LIMNODRILUS UDEKEMIANUS CLAPARÈDE.

Les expériences avec *Limnodrilus udekemianus* ont été entreprises au mois d'avril et de mai de 1929. Je les ai répétées avec un matériel moins nombreux au mois de décembre de 1929 et en octobre de 1931. Le tableau III en donne les protocoles abrégés.

Chez cette espèce l'appareil génital se développe dans les conditions de laboratoire assez rapidement (8—13 jours après l'isolation).

Au total 31 individus isolés ont atteint la maturité sexuelle au cours de mes expériences. Sur 130 cocons pondus chez 70[1] j'ai suivi leur développement jusqu'à l'éclosion des jeunes vers. Dans 65 cocons (92,8 %) les œufs se sont développés.

[1] Les autres ont été fixés.

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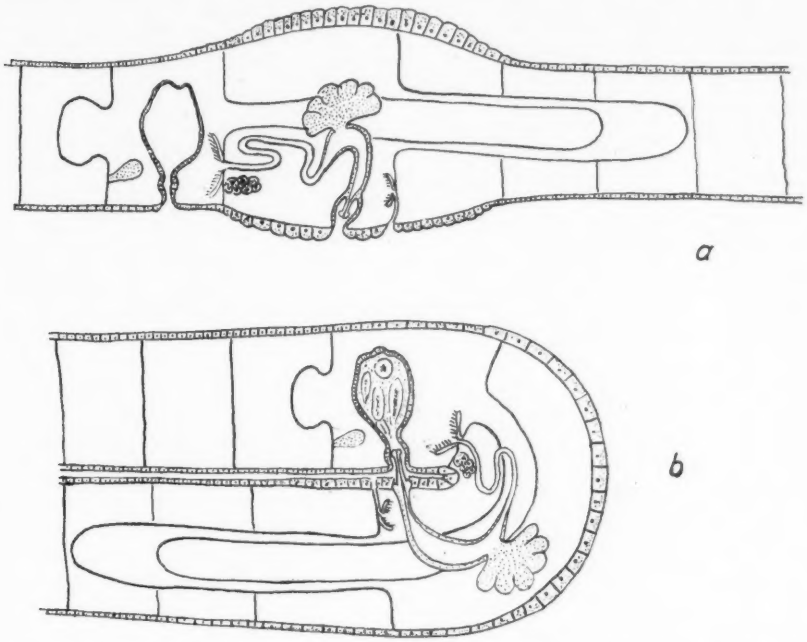

Fig. 1. Le mécanisme probable d'autocopulation chez *Limnodrilus udekemianus* (schema). *a.* État normal. *b.* Autocopulation.

Les cocons pondus étaient de forme ovale et d'assez petites dimensions (0,9 mm. sur 0,5 mm.). Souvent ils n'étaient pas enveloppés de vase de sorte qu'on pouvait établir précisément le nombre initial d'œufs. Ordinairement chaque cocon ne contenait que 2 œufs (0,3—0,5 mm. environ), plus rarement 1 ou 3.

La présence des spermatophores dans les spermathèques a été constatée chez tous les individus isolés, qui étaient fixés et debités en série. La fécondation croisée étant absolument impossible chez les exemplaires en question, le phénomène mentionné ci-dessus, comme je l'ai déjà indiqué (1931), ne peut être expliqué que par l'autocopulation. La fig. 1. nous montre le mécanisme probable.

Comme chez tous les représentants du genre *Limodrilus* les organes copulatifs de *L. udekemianus* sont placés sur la face ventrale du segment XI. Les orifices des spermathèques se trouvent sur la face ventrale du segment X. Si le corps se recourbe entre les deux paires d'orifices, les courts penis érectiles peuvent sans doute être introduits dans les canaux des réceptacles séminaux. Il faut admettre que ce processus peut s'effectuer plusieurs fois, puisque dans les ampoules des réceptacles j'ai souvent trouvé des quantités considérables de spermatophores.

Tableau III.

Protocoles des expériences avec *Limnodrilus udekemianus* Clap.

Individu No	Localité	Date de capture	Date d'isolation	Nombre de cocons pondus	Nombre de cocons dont le développement a été suivi (Index en haut désigne le nombre d'œufs dans le cocon)	Nombre de cocons aux embryons développés	Date de fixation du ver	Contenu des spermathèques (d'après les préparations)
1	Újezd nad Lesy (étang)	20. V. 29	22. V. 29	3	I^2, II^2, III^2	I^2, II^2, III^2	11. VI. 29	Spermatophores
2	„ „ „ „	„	„	2	—	—	21. VI. 29	„
3	„ „ „ „	„	„	8	I^2, II^2, III^2, IV^2, V^2	I^2, II^1, III^2	17. VI. 29	„
4	„ „ „ „	„	„	9	I^2, II^2, III^2, IV^2, V, VI^2	I^2, II^2, III^2, IV^2, V^1, VI^2	„	„
5	„ „ „ „	„	„	9	I^2, II, III^1, IV^1, V^1, VI^1	I^2, II^2, III^1, IV^1, V^1, VI^1	„	„
6	„ „ „ „	„	23. V. 29	5	I^2, II^2, III^2, IV^2, V^2	I^2, II^2, III^2, IV^2, V^2	13. VI. 29	„
7	„ „ „ „	„	„	12	I^2, II^2, III^2, IV, V, VI^2, VII	I^2, II^2, III^2, IV^2, V^3, VI^2, VII^2	18. VI. 29	„
8	„ „ „ „	„	24. V. 29	5	I^3, II, III, IV, V	I^3, II^3, III^2, IV^2, V^2	14. VI. 29	„
9	„ „ „ „	„	„	8	I, II, III, IV, V, VI, VII, VIII	I^2, II^2, III^2, IV^3, V^2, VI^2, VII^2, $VIII^2$	„	„
10	„ „ „ „	„	„	6	I, II	I^2, II^2	„	„
11	„ „ „ „	„	„	—	—	—	„	„
12	„ „ „ „	„	„	5	I, II, III^2	I^2, II^2, III^2	24. VI. 29	„
13	„ „ „ „	„	„	4	—	—	„	„
14	„ „ „ „	„	„	4	I^1, II^1	I^1, II^1	14. VI. 29	„

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15	„	„	„	„	„	25. V. 29	8	I, II, III, IV, V, VI	I^2, II^1, III^1, IV^2, V^2, VI^2	15. VI. 29	„
16	„	„	„	„	„	„	6	I, II, III, IV	I^2, II^2, III^1, IV^2	„	„
17	„	„	„	„	„	„	2	—	—	14. VI. 29	„
18	„	„	„	„	„	29. V. 29	1	I	I	19. VI. 29	„
19	„	„	„	„	„	„	—	—	—	15. VI. 29	„
20	„	„	„	„	„	„	2	—	—	17. VI. 29	„
21	„	„	„	„	„	„	1	—	—	„	„
22	„	„	„	„	„	„	2	I, II	—	1. VII. 29	„
23	„	„	„	„	„	„	7	—	—	25. VI. 29	„
24	„	„	„	„	„	31. V. 29	—	—	—	17. VI. 29	„
25	„	„	„	„	„	„	4	—	—	25. VI. 29	„
26	„	„	„	„	„	„	1	—	—	17. VI. 29	„
27	„	„	„	„	„	„	4	I	I	21. VI. 29	„
28	„	„	„	„	1. IV. 29	15. IV. 29	3	I^2	I^2	4. V. 29	„
29	„	„	„	„	1. XII. 29	6. XII. 29	2 (infection)	—	—	8. I. 30	„
30	„	„	„	„	„	3. XII. 29	6	I^2, II^2	I^2, II^1	17. I. 30	„
31	Strašnice (étang)				29. X. 31	29. XII. 31	1	I	—	10. XI. 31	„
Nombre total de cocons:							130	70	65 (92,8 %)		

B. LIMNODRILUS HOFFMEISTERI CLAPARÈDE.

J'ai entrepris avec *Limnodrilus hoffmeisteri* deux séries d'expériences:

1) Pour établir, si les œufs de cette espèce peuvent se développer sans être fertilisés par le sperme d'un autre individu.

2) Pour étudier les processus d'expulsion des globules polaires dans les œufs, pondus par les individus qui n'avaient pas copulé ainsi que dans les œufs fertilisés. Au cours de la seconde série d'expériences, tout en étudiant ce problème principal, j'ai pu établir pendant une assez longue période de temps les intervalles entre les pontes successives.

La première série d'expériences a été réalisée en 1929 (avril, mai, novembre, décembre) — en même temps que les expériences avec *L. udekemianus*. Le tableau IV en donne les protocoles abrégés.

La durée de la période pendant laquelle les individus isolés de *L. hoffmeisteri* atteignent la maturité sexuelle, varie beaucoup dans les conditions de laboratoire (14—30 jours).[1]

J'ai déjà publié (1931) les résultats de la première série d'expériences. Il a été constaté que les œufs de *L. hoffmeisteri* sont capables de se développer et de donner des individus tout à fait normaux sans être fertilisés par le sperme d'un autre individu.

Au cours de la première série d'expériences j'ai réussi à élever jusqu'à maturité sexuelle 51 exemplaires qui ont déposé ensemble 283 cocons. Sur 226 cocons, que j'ai laissés se développer, seulement 129 (57 %) ont donné de jeunes individus. Je ne donne que le pourcentage des cocons qui ont achevé leur développement. Il a été impossible d'établir le pourcentage d'œufs développés, leur nombre dans chaque cocon étant souvent difficile à signaler à cause de la vase qui rendait les cocons non-transparents. On peut pourtant supposer que dans la plupart des cas tous les œufs du même cocon éprouvent le même sort.[2]

Les cocons ovales de *L. hoffmeisteri* sont plus volumineux que ceux de *L. udekemianus* (1,2—1,6 mm. sur 0,8 mm.) et renferment un nombre très variable d'œufs (leur diamètre mesure 0,3—0,5 environ). Le nombre moyen constaté au cours de mes expériences est 4—7 œufs, le maximum étant 13, le minimum 1.

Chez les individus isolés de *L. hoffmeisteri*, qui ont ensuite pondu des cocons capables de se développer

[1] Au cours de mes expériences j'ai aussi réussi à faire quelques observations sur le développement du penis chez cette espèce. Le tube chitineux de cet organe apparait d'abord sous forme d'une courte ébauche à bout distal déjà formé. Il grandit et atteint peu à peu ses dimensions normales. Je n'ai pas encore étudié le processus, dont la marche est la même chez *L. claparedeianus*, du point de vue histologique.

[2] J'ai pourtant constaté des cas, où, autant que j'aie pu le suivre, seulement une partie des œufs se développait.

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je n'ai jamais pu constater la présence de spermatophores dans les réceptacles séminaux. Les ampoules de ces organes contenaient une secrétion homogène de caractère muqueux qui se colorait intensivement par l'éosine. En cas de copulation cette sécrétion donne probablement la couche externe des spermatophores. Nos constatations prouvent que le processus d'autocopulation, signalé chez *L. udekemianus,* n'existe pas chez *L. hoffmeisteri.*

La seconde série d'expériences a été commencée en octobre 1931. J'en donne les résultats essentiels dans un autre chapitre du présent mémoire. Ici je ne veux qu'exposer certaines observations relatives au processus de ponte chez les individus fécondés et non fécondés.

Les uns et les autres déposaient les cocons pendant le jour aussi bien que dans la nuit. Quant à la fréquence des pontes chez les individus fertilisés et chez les exemplaires qui n'avaient pas copulé, j'ai pu observer au cours de mes expériences une grande différence entre ces deux catégories. Tandis que 26 exemplaires[1] isolés avant leur maturité sexuelle n'ont pondu au mois de décembre de 1931 que 74 cocons au total, le même nombre d'exemplaires fertilisés, élevés dans le récipient commun ont éliminé 150 cocons. Les exemplaires qui n'avaient pas copulé n'ont donc pondu que 48 % des cocons déposés par le même nombre de vers fécondés. Pendant la première moitié de janvier 1932[2] 25 exemplaires isolés ont pondu 20 cocons, tandis que 22 individus élevés dans le récipient commun en ont deposé 39. Chez les exemplaires qui n'avaient pas copule, l'intervalle entre les deux pontes successives a été extrêmement variable, de sorte qu'aucune régularité n'ait pu être établie. Le tableau V résume les protocoles de nos expériences (II[e] série).

On peut donc dire qu'au cours de cette série d'expériences on a pu observer chez les individus non fécondés une tendance bien prononcée de ralentir leurs pontes. Quelquefois la rétention de l'élimination des œufs déjà développés dans les ovisacs durait très longtemps et l'appareil génital de pareils exemplaires commençait enfin à dégénérer. On peut supposer que ce retardement de ponte chez les exemplaires isolés avant leur maturité sexuelle, était dû à l'absence de spermatophores dans les spermathèques. Chez les exemplaires fertilisés, élevés dans les mêmes conditions, les pontes ont été, comme nous l'avont dit, beaucoup plus intensives. Pourtant on ne peut pas affirmer que l'absence de sperme dans les spermathèques soit la seule cause déterminant le retardement en question. J'ai eu l'occasion de signaler le même phénomène chez les individus fertilisés qui pourtant au moment de l'isolation, il faut le noter, n'avaient plus de spermatophores aux contours nets. Cependant dans d'autres cas, chez les individus fertilisés, les pontes étaient régulières et

[1] D'entre eux ont été pourtant fixés encore avant le 1er janvier 1932. Ils ont pondu très peu de cocons (Tab. V, 1, 3, 9). No 16 n'est pas pris en considération.

[2] Jusqu'à 12. I. 1932.

Tableau IV.

Protocoles des expériences, avec *Limnodrilus hoffmeisteri* Clap. Ire série (1929).

Individu No	Localité	Date de capture	Date d'isolation	Nombre total de cocons pondus	Nombre de cocons déstinés au développement (Index indique le nombre d'œufs dans chaque cocon)	Nombre de cocons aux embryons dévoloppés	Date de fixation du ver	Spermathèques
1	Běchovice (mare)	1. IV. 29	6. IV. 29	5	I^3, II^3, III^3, IV^2	I^1, II^2, III^3	7. V. 29	Pas de spermatoph.
2	„ „	„	8. IV. 29	5	I^2, II^4, III^4, IV^2	I^1, II^4, III^4	16. V. 29	„ „ „
3	„ „	„	9. IV. 29	4	I^3, II^2	I^3, II^1	21. V. 29	„ „ „
4	Újezd nad Lesy (étang)	20. V. 29	21. V. 29	2	I^5, II^3	—	5. VI. 29	„ „ „
5	„ „ „ „	„	„	3	I, II	—	1. VII. 29	„ „ „
6	„ „ „ „	„	23. V. 29	2	I^4, II^1	—	24. VI. 29	„ „ „
7	Běchovice (mare)	1. IV. 29	9. IV. 29	10	I^2, II^2	I^2, II^2	8. V. 29	„ „ „
8	„ „	„	10. IV. 29	2	—	—	6. V. 29	„ „ „
9	„ „	„	„	4	I^2	I^1	2. V. 29	„ „ „
10	Újezd nad Lesy (étang)	20. V. 29	24. V. 29	3	I^7, II	I^6	24. VI. 29	„ „ „
11	„ „ „ „	„	„	3	I^3, II^3, III^3	I^3, II^4, III^3	21. VI. 29	„ „ „
12	„ „ „ „	1. IV. 29	10. IV. 29	1	—	—	29. V. 29	„ „ „
13	„ „ „ „	20. V. 29	25. V. 29	2	I^5, II^4	—	21. VI. 29	„ „ „
14	„ „ „ „	„	29. V. 29	1	I^3	—	1. VII. 29	„ „ „
15	„ „ „ „	1. IV. 29	16. IV. 29	3	I, II, III	I^1	23. V. 29	„ „ „
16	„ „ „ „	„	18. IV. 29	3	I, II, III	—	„	„ „ „
17	„ „ „ „	„	„	1	I	I	16. V. 29	„ „ „
18	„ „ „ „	20. V. 29	31. V. 29	1	I	—	1. VII. 29	„ „ „
19	Mokropsý (fl. Berounka)	27. X. 29	29. X. 29	11	I^5, II^7, III^9, IV, V, VI, VII, VIII, IX, X, XI	I^5, II^7, III^5	30. I. 30	„ „ „
20	Újezd nad Lesy (étang)	12. XI. 29	20. XI. 29	10	I^9, II, III^4, IV^6, V^6, VI^5, VII^6, VIII	I^9, II^7, III^4, IV^6, V^6, VI^5, VII^6, $VIII^8$	11. II. 30	„ „ „
21	„ „ „ „	1. XII. 29	3. XII. 29	8	I^6, II^6, III^4, IV^4, V^6, VI^3, VII^6, $VIII^6$	I^6, II^6, III^4, IV^4, V^6, VI^3, VII^6	7. II. 30	„ „ „
22	„ „ „ „	„	„	9	I^6, II^5, III^4, IV^5, V^6, VI^5, VII, $VIII^7$	I^3, II^5, III^4, IV^2, V^6, VI^5, $VII^{1+3(7)}$, $VIII^7$	10. II. 30	„ „ „
23	Mokropsý (fl. Berounka)	27. X. 29	4. XI. 29	2	I^6, II	—	20. XII. 29	„ „ „
24	„ „ „	„	5.	7	I, II^{10}, III^8, IV^9, V^9, VI, VII	I^2, II^{10}, III^8, IV^9, V^9	28. I. 30	„ „ „

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25	Ujezd nad Lesy (étang)				1. XII. 29	10. XII. 29	2	I^6, II^2	—	„	„ „ „
26	„	„	„	„	„	3. XII. 29	8	I^1, II^3, III, IV, V	I^1, II^1	„	„ „ „
27	„	„	„	„	„	10. XII. 29	4	I^7, II^4	I^7, II^3	„	„ „ „
28	„	„	„	„	3. XI. 29	6. XI. 29	13	I^4, II, III^4, IV^3, V^6, VI, VII	I^4, II^1, III^4, IV^3, V^5	17. III. 30	Dégénérescence
29	„	„	„	„	„	„	12	I^1, II, III, IV, V, VI	I^4, II^1	„	Pas de spermatoph.
30	„	„	„	„	1. XII. 29	3. XII. 29	6	I^2, II, III, IV, V	I^2	13. I. 30	„ „ „
31	„	„	„	„	3. XI. 29	9. XI. 29	11	I, II^5, III^5, IV, V, VI, VII, VIII, IX^4, X	I^1, II^3	20. XII. 30	„ „ „
32	„	„	„	„	1. XII. 29	3. XII. 29	8	I^3, II, III, IV, V, VI, VII, VIII	I^3, II^2	15. I. 30	„ „ „
33	„	„	„	„	3. XI. 29	9. XI. 29	7	I^4, II^3, III^4, IV^9, V, VI^4, VII^3	I^4, II^3, III^3	20. XII. 30	„ „ „
34	„	„	„	„	1. XII. 29	10. XII. 29	4	I, II^4, III	I^2, II^4	30. I. 30	„ „ „
35	„	„	„	„	3. XI. 29	9. XI. 29	7	I^4, II^3, III^6, IV^4, V^2, VI^4	I^4, II^3, III^6, IV^4	7. I. 30	Dégénérescence
36	„	„	„	„	12. XI. 29	20. XI. 29	5	I^2, II, III, IV, V	—	13. I. 30	„
37	„	„	„	„	„	„	9	I^3, II, III, IV, V, VI, VII, VIII, IX^4	I^3, II^3, III^3, IV^3, V^4, VI^2, VII^3, $VIII^2$	8. I. 30	Pas de spermatoph.
38	„	„	„	„	1. XII. 29	6. XII. 29	2	I, II	—	23. I. 30	„ „ „
39	„	„	„	„	„	„	19	I, II, III, IV, V, VI, VII, VIII, IX, X, XI, XII, XIII	I^1, II, III, IV, V, VI, VII, $VIII^2$, IX^4	17. III. 30	„ „ „
40	„	„	„	„	„	„	4	I^7, II, III^4, IV	I^7, II^2, III^4	27. I. 30	„ „ „
41	„	„	„	„	„	„	4	I^6, II^6, III^4, IV^5	I^6	6. I. 30	„ „ „
42	„	„	„	„	„	„	10	I^5, II^5, III^5, IV^5, V^6, VI^5, VII^7, $VIII^6$, IX^7, X	I^5, II^5, III^2, IV^5, V^6, VI^5, VII^7, $VIII^6$, IX^7	11. II. 30	„ „ „
43	„	„	„	„	„	7. XII. 29	8	I^5, II^6, III^6, IV^5, V^3, VI, VII, VIII	I^2, II^6, $III,^6$ IV^5, V^3	10. II. 30	? (Préparation gatée
44	„	„	„	„	„	„	6	I^5, II^4, III^3, IV^5, V	I^5, II^4, $III,^3$ IV^5, V^4	21. I. 30	Pas de spermatoph.
45	„	„	„	„	„	„	3	I^5, II, III	I^5	„	„ „ „
46	„	„	„	„	„	„	2	I^2, II^6	I^2, II^6	11. II. 30	„ „ „
47	„	„	„	„	„	„	5	I^5, II^6, III, IV, V	I^5, II^6, III^3	6. II. 30	„ „ „
48	„	„	„	„	„	„	5	I^2, II^3, III^5, IV^6, V^4	I^2, II^3, III^4, IV^6	27. I. 30	? (Préparation gatée)
49	„	„	„	„	„	17. XII. 29	3	I^9, II^{11}	I^9, II^{11}	10. II. 30	Dégénérescence
50	„	„	„	„	„	„	9	I^{13}, II^2, III, IV	I^{13}, II^2	17. III. 30	„
51	„	„	„	„	„	„	5	I, II^3, III, IV, V	I^2, II^3	29. I. 30	Pas de spermatoph.
Nombre total de cocons:							283	226	129 (57 %)		

Tableau

Protocoles des expériences avec *Limnodrilus*

Entre les parenthèses sont indiquées les intervalles

Individu No	Localité	Date de capture	Date d'isolation	Devenu sexuellement mûr	Dates			
					I.	II.	III.	IV.
1	Strašnice (étang)	29. X. 31	10. XI. 31	27. XI. 31	17. XII. 31	—	—	—
2	Mokropsý (fl. Berounka)	17. X. 31	26. X. 31	„	7. XII. 31	—	—	—
3	„ „ „	„	27. X. 31	28. XI. 31	? 5. XII. 31	7. XII. 31 (? 2)	—	—
4	Strašnice (étang)	29. X. 31	10. XI. 31	?	?	?	? 27. XI. 31	6. XII. 31 (? 9)
5	Újezd nad Lesy (étang)	14. XI. 31	16. XI. 31	5. XII. 31	10. XII. 31	12. XII. 31 ($1^1/_2$)	20. XII. 31 (8)	24. XII. 31 ($4^1/_2$)
6	„ „ „ „	„	„	27. XI. 31	?	13. XII. 31 (?)	16. XII. 31 (3)	—
7	„ „ „ „	„	„	6. XII. 31	15. XII. 31	19. XII. 31 (4)	23. XII. 31 (4)	8. I. 32 ($15^1/_2$)
8	„ „ „ „	„	„	2. XII. 31	„	18. XII. 31 (3)	30. XII. 31 (12)	8. I. 32 (9)
9	„ „ „ „	„	17. XI. 31	8. XII. 31	18. XII. 31	—	—	—
10	„ „ „ „	„	„	7. XII. 31	? 13. XII. 31	6. I. 32 (? 23)	—	—
11	„ „ „ „	„	„	4. XII. 31	23. XII. 31	—	—	—
12	„ „ „ „	„	„	8. XII. 31	?	15. XII. 31	19. XII. 31 (4)	23. XII. 31 ($3^1/_2$)
13	„ „ „ „	„	„	2. XII. 31	5. XII. 31	13. XII. 31 ($8^1/_2$)	20. XII. 31 (7)	30. XII. 31 (10)
14	„ „ „ „	„	„	28. XI. 31	15. XII. 31	30. XII. 31 ($14^1/_2$)	—	—
15	„ „ „ „	„	„	7. XII. 31	?	15. XII. 31	17. XII. 31 ($2^1/_2$)	19. XII. 31 ($2^1/_2$)
16	„ „ „ „	„	„	8. XII. 31	? 14. XII. 31	15. XII. 31 (? 1)	—	—
17	„ „ „ „	„	„	27. XI. 31	7. XII. 31	12. XII. 31 (5)	28. XII. 31 ($16^1/_2$)	—
18	„ „ „ „	„	„	5. XII. 31	? 15. XII. 31	22. XII. 31 (? 7)	—	—
19	„ „ „ „	„	„	27. XI. 31	15. XII. 31	26. XII. 31 (11)	29. XII. 31 ($2^1/_2$)	4. I. 31 (6)
20	„ „ „ „	„	„	7. XII. 31	? 13. XII. 31	18. XII. 31 ($5^1/_2$)	23. XII. 31 ($4^1/_2$)	30. XII. 31 ($6^1/_2$)
21	„ „ „ „	„	„	8. XII. 31	17. XII. 31	20. XII. 31 (3)	30. XII. 31 ($10^1/_2$)	—
22	„ „ „ „	„	„	„	? 15. XII. 31	17. XII. 31 (? 2)	19. XII. 31 ($2^1/_2$)	28. XII. 31 ($8^1/_2$)
23	„ „ „ „	„	„	7. XII. 31	? 13. XII. 31	—	—	—
24	„ „ „ „	„	„	5. XII. 31	19. XII. 31	23. XII. 31 (4)	8. I. 32 (16)	—
25	„ „ „ „	„	„	?	? 24. XII. 31	31. XII. 31 (? 7)	9. I. 32 ($9^1/_2$)	3. II. 32 ($24^1/_2$)
26	„ „ „ „	„	„	8. XII. 31	14. XII. 31	18. XII. 31 (4)	28. XII. 31 (10)	5. I. 32 (8)
27	„ „ „ „	„	28. XI. 31	15. XII. 31	24. XII. 31	28. XII. 31 ($3^1/_2$)	5. I. 32 ($7^1/_2$)	19. I. 32 (14)
28	„ „ „ „	„	17. XI. 31	?	?	?	?	?

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V.

hoffmeisteri Clap. IIe série (1931—32).

entre les dates de pontes successives.

de pontes								Sort du ver
V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	
—	—	—	—	—	—	—	—	Régression de l'appareil génital 22. XII. 31
—	—	—	—	—	—	—	—	Régression de l'appareil génital 12. I. 32
—	—	—	—	—	—	—	—	Régression de l'appareil génital 25. XII. 31
17. XII. 31 (11)	—	—	—	—	—	—	—	Régression de l'appareil génital 29. XII. 31
30. XII. 31 ($5^1/_2$)	5. I. 32 ($6^1/_2$)	7. I. 32 (2)	—	—	—	—	—	Observations terminées 12. I. 32
—	—	—	—	—	—	—	—	Périt 31. XII. 31
—	—	—	—	—	—	—	—	Observations terminées 12. I. 32
12. I. 32 (4)	—	—	—	—	—	—	—	Observations terminées 12. I. 32
—	—	—	—	—	—	—	—	Fixé 25. XII. 31
—	—	—	—	—	—	—	—	Observations terminées 12. I. 32
—	—	—	—	—	—	—	—	Observations terminées 12 I. 32
30. XII. 31 ($7^1/_2$)	—	—	—	—	—	—	—	Fixé 12. I 32.
5. I. 32 (6)	—	—	—	—	—	—	—	Régression de l'appareil génital 22. I. 32
—	—	—	—	—	—	—	—	Régression de l'appareil génital 22. I. 32
29. XII. 31 ($9^1/_2$)	30. XII. 31 ($1^1/_2$)	12. I. 32 (13)	15. I. 32 (3)	—	—	—	—	Régression de l'appareil génital 22. I. 32
—	—	—	—	—	—	—	—	Périt 17. XII. 31
—	—	—	—	—	—	—	—	Observations terminées 12. I. 32
—	—	—	—	—	—	—	—	Régression de l'appareil génital 22. I. 32
—	—	—	—	—	—	—	—	Périt 11. I. 32
5. I. 32 (6)	8. I. 32 (3)	9. I. 32 (1)	—	—	—	—	—	Observations terminées 12. I. 32
—	—	—	—	—	—	—	—	Observations terminées 17. I. 32
5. I. 32 (8)	17. I. 32 (12)	—	—	—	—	—	—	Fixé 22. I. 32
—	—	—	—	—	—	—	—	Fixé 22. I. 32 (parasites)
—	—	—	—	—	—	—	—	Fixé 22. I. 32
5. II. 32 ($2^1/_2$)	6. II. 32 (1)	9. II. 32 (3)	—	—	—	—	—	Observations terminées 10. II. 32
12. I. 32 (7)	22. I. 32 (10)	25. I. 32 (3)	27. I. 32 (2)	4. II. 32 ($7^1/_2$)	5. II. 32 (1)	6. II. 32 (1)	7. II. 32 (1)	Observations terminées 10. II. 32
22. I. 32 (3)	24. I. 32 ($1^1/_2$)	1. XII. 32 (8)	5. II. 32 (4)	—	—	—	—	Observations terminées 7. II. 32
?	5. I. 32	9. I. 32 (4)	—	—	—	—	—	Fixé 22. I. 32

separées de courts intervalles (2—4 jours). Chez les individus qui n'avaient pas copulé, je n'ai jamais observé de pareils intervalles courts et réguliers entre les pontes successives. Malheureusement je n'ai pas eu la possibilité d'étudier ce problème d'une façon précise, une longue série d'expériences parallèles avec les individus isolés à l'état fécondé étant indispensable pour ce but. Ceux dont j'ai disposé ont été très peu nombreux.

C. LIMNODRILUS CLAPAREDEIANUS RATZEL.

Avec *Limnodrilus claparedeianus* j'ai entrepris beaucoup moins d'expériences qu'avec les deux espèces précédentes. Les protocoles de ces expériences sont donnés dans le tableau VI. La série réalisée en 1929 (avril, octobre) fait voir seulement 12 individus isolés, qui avaient atteint la maturité sexuelle. Les résultats, que j'ai obtenus, ont été confirmés plus tard (novembre 1931) encore par deux cas pareils. Il s'accordent complètement avec ceux qui sont signalés chez *L. hoffmeisteri*.

Nous sommes de nouveau en présence de la faculté de déposer les cocons dont les œufs se développent sans être fertilisés par les spermatozoïdes d'un autre individu.

Du nombre total de 84 cocons déposés par 14 individus isolés, j'ai laissé pour les observations ultérieures 53 cocons.[1] Les jeunes individus se sont développés dans 25 d'entre eux (47,2 %).

Les cocons de *L. claparedeianus* ont à peu près les mêmes dimensions que ceux de *L. hoffmeisteri* (1—1,3 mm. sur 0,9 mm.). Quant au nombre d'œufs (0,3—0,5 mm. de diamètre environ) il variait beaucoup au cours de mes expériences. Il y avait le plus souvent de 3 à 7 œufs, le nombre minimal étant 2, le maximum 11. Généralement les cocons ont été couverts de vase, de sorte qu'il était impossible d'en établir le nombre initial.

Dans les conditions de laboratoire la durée de développement de l'appareil génital chez *L. claparedeianus* varie considerablement (de 13 à 30 jours après l'isolation).

Etudiées sur coupes, les spermathèques des individus isolés, qui avaient éliminé des œufs capables de se développer, n'ont pas présenté de spermatophores. De même que chez *L. hoffmeisteri* les ampoules de ces organes renfermaient une secrétion muqueuse. Il s'en suit que l'autocopulation n'existe pas chez cette espèce et qu'il faut chercher ici, de même que chez *L. hoffmeisteri* une autre explication de la faculté des œufs de se développer sans fécondation réciproque.

[1] Les autres cocons ont été fixés.

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Tableau VI.

Protocoles des expériences avec *Limnodrilus claparedeianus* RATZEL.

Individu No	Localité	Date de capture	Date d'isolation	Nombre de cocons pondus	Nombre de cocons destinés au développement (Index indique le nombre d'œufs dans chaque cocon)	Nombre de cocons développés	Date de fixation du ver	Receptacula seminis
1	Běchovice (mare)	1. IV. 29	8. IV. 29	4	I, II	—	5. VI. 29	Pas de spermatoph.
2	„ „	„	9. IV. 29	1	—	—	22. VI. 29	„ „ „
3	Mokropsý (fl. Berounka)	17. IV. 29	25. IV. 29	3	I^{3}, II^{4}, III	I^{3}, II^{4}	21. V. 29	„ „ „
4	„ „ „	„	„	10	I^{5}, II^{2}, III, IV, V, VI	I^{3}, II^{2}	11. VI. 29	„ „ „
5	„ „ „	„	29. IV. 29	2	I, II	I	23. V. 29	„ „ „
6	„ „ „	„	30. IV. 29	1	I	—	24. V. 29	„ „ „
7	„ „ „	„	18. IV. 29	2	I^{5}, II^{6}	I^{5}, II	25. V. 29	„ „ „
8	„ „ „	„	22. IV. 29	14	I^{7}, II, III^{4}, IV, V, VI, VII	I^{7}, II^{2}, III^{4}	21. VI. 29	„ „ „
9	„ „ „	„	23. IV. 29	2	I^{5}, II	I^{5}	23. V. 29	„ „ „
10	„ „ „	27. X. 29	30. X. 29	8	I^{3}, II, III^{7}, IV, V, VI, VII, VIII	I^{3}, II^{5}, III^{6}	20. XII. 29	„ „ „
11	„ „ „	„	31. X. 29	6	I^{6}, II, III, IV	—	7. I. 30	„ „ „
12	„ „ „	„	5. XI. 29	7	I^{9}, II^{11}, III, IV, V, VI, VII	I^{8}, II^{11}, III^{8}, IV^{8}	20. XII. 29	„ „ „
13	Čelakovice (mare)	15. XI. 31	16. X. 31	15	I, II^{9}, III^{10}, IV^{7}, V^{8}, VI, VII	I^{10}, II^{3}, III^{10}, IV^{7}, V^{7}	8. XII. 31	„ „ „
14	„ „	„	„	9	I^{5}, II^{2}	I^{5}, II^{2}	9. XII. 31	„ „ „
Nombre total de cocons:				84	53	25 (47.2 %)		

Tableau VII.

Protocoles des expériences avec *Rhynchelmis limosella* HOFFMSTR.

Localité — Čelakovice (fossés).

Individu No	Date de capture	Date d'isolation	Cocons trouvés	Nombre de cocons pondus (Index désigne le nombre d'œufs dans le cocon)	Cocons présentant les premiers stades de segmentation (—) = in vico (+) = d'après les préparations	Sort du ver	Spermathèques
1	2. XI. 31	3. XI. 31	30. III. 32	I^3, II, III	I^1(—)	Fixé 30. III. 32	Régression
2	18. X. 31	20. X. 31	„	I^6, II^{14}, III	I^6(+) ; II^{14}(+)	Fixé 8. IV. 32	Pas de sperme
3	2. XI. 31	3. XI. 31	2. IV. 32	I	—	Laissé pour les expériences ultérieures	?
4	„	„	30. III. 32	I^3	I^3(—)	Fixé 13. IV. 32	Régression
5	„	12. XI. 31	31. III. 32	I	—	Laissé pour les expériences ultérieures	?
6	„	„	„	I^6	—	Périt 1. IV. 32	?

D. RHYNCHELMIS LIMOSELLA HOFFMEISTER.

Quoique j'aie utilisé un matériel relativement abondant, il faut reconnaître, que les résultats de mes expériences avec *Rhynchelmis limosella* (protocoles — tableau VII) ne nous donnent qu'une orientation préliminaire dans le problème en question. On peut faire quelque constatations mais elles devraient encore être confirmées par de nouvelles recherches.

On peut résumer les résultats obtenus en trois thèses:

1) Les individus de *Rhynchelmis limosella,* devenus sexuellement mûrs en état isolé, toute possibilité d'accouplement étant ainsi exclue, sont capables d'éliminer les œufs.

2) On n'observe ce phénomène que dans des cas rares. Un grand pourcentage de ces individus subissent la régression physiologique de l'appareil génital sans avoir déposé de cocons.

3) Les œufs des cocons, pondus par les individus, qui avaient atteint la maturité sexuelle en état isolé, sont capables de se segmenter. Autant que je l'ai pu constater, me basant sur un nombre très restreint d'observations, la segmentation ne dépasse pas les premiers stades. Elle arrête ensuite sa marche et les œufs périssent.

Les deux premières constatations concordent avec les résultats obtenus par Mr le Prof. V. JANDA que j'ai mentionnés ci-dessus.

Du nombre total de 76 exemplaires isolés au mois de novembre 1931, 35 ont atteint la maturité sexuelle au mois de mars 1932. Vers la fin du mois, quand le temps est devenu plus chaud, 6 d'entre eux ont déposé des cocons (10 au total). Quatres individus ont éliminé 1 cocon chacun, deux individus 3 cocons chacun.

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Le sort de ces cocons a été le suivant:

Cocon N° 1 (Tableau VII, individu I, cocon I)	Segmentation constatée in vivo. Les cocons périrent 3—4 jours après l'élimination.
Cocon N° 2 (Tab. VII, ind. 4, cocon I)	
Cocon N° 3 (Tab. VII, ind. 2, cocon I)	Segmentation constatée in vivo, l'examen de la préparation l'a confirmé.
Cocon N° 4 (Tab. VII, ind. 2, cocon II)	Examinés in vivo, les œufs paraissent ne pas se segmenter. Examen des préparations prouve la segmentation.
Cocon N° 5 (Tab. VII, ind. 6, cocon I)	Examinés in vivo, les œufs paraissent ne pas se segmenter. Périrent 4 jours après la ponte.
Cocon N° 6 (Tab. VII, ind. 1, cocon II)	Gaine, couverte de vase a rendu impossible l'examen du contenu des cocons. Les œufs ont péri 3—4 jours après la ponte.
Cocon N° 7 (Tab. VII, ind. 1, cocon III)	
Cocon N° 8 (Tab. VII, ind. 2, cocon III)	
Cocon N° 9 (Tab. VII, ind. 3, cocon I)	
Cocon N° 10 (Tab. VII, ind. 5, cocon I)	

Au commencement du mois d'avril une prompte régression de l'appareil génital s'est fait voir chez tous les exemplaires sexuellement mûrs.

Au cours de cette série d'expériences avec *Rhynchelmis limosella* je n'ai pas pu constater si l'autocopulation existe chez cette espèce. De 6 exemplaires qui avaient déposé des cocons j'en ai fixé seulement trois. Chez deux d'entre eux (N° 1 et N° 4) les spermathèques ont été fortement dégénérées. Chez le troisième individu (N° 2) elles étaient encore présentes. Je n'y ai pus trouvé de sperme. Il parait que cette observation prouve qu'il n'y a pas d'autocopulation chez cette espèce. Un exemplaire (N° 6) a péri et s'est décomposé dans l'eau avant que j'aie pu le fixer. J'ai laissé en état isolé les deux derniers exemplaires (N° 3 et N° 5) pour continuer les expériences.

E. EISENIELLA TETRAEDRA FORMA TYPICA (SAVIGNY).

Je n'ai eu qu'un nombre restreint d'individus d'*Eiseniella tetraedra* propres à l'isolation, de sorte qu'à l'heure actuelle mes expériences avec cette espèce doivent être considérées comme préliminaires. Néanmoins les résultats sont ici beaucoup plus nets que chez *Rhynchelmis limosella*.

Chez *Eiseniella tetraedra f. typica*, comme chez d'autres espèces que j'ai étudiées, j'ai pu constater le développement des œufs non fertilisés par le sperme d'un autre individu. Le développement continue sa marche jusqu'à la fin et les jeunes exemplaires, éclos des cocons, sont tout à fait normaux.

A la fin du mois d'octobre et au commencement de novembre j'ai isolé au total 19 exemplaires immatures d'*Eiseniella tetraedra*. Pendant l'hiver (décembre, fevrier) seulement 4 d'entre eux ont atteint la maturité sexuelle et déposé au total 49 cocons dont 47 ont été laissés pour les observations ultérieures. Ces cocons (1,8 mm. sur 1,2 mm.), ovales ou arrondis, sont de couleur jaune-verdâtre et renferment toujours 1 œuf. Grâce à la gaine transparente on a pu observer même les stades initiaux de développement relévés par l'apparition d'un disque sombre qui s'allongeait peu à peu et prenait la forme de ver. De jeunes vers se sont développés dans 42 cocons (86 % des cocons soumis à l'observation).

Dans les spermathèques de trois individus (N^{os} 2, 3, 4) une sécrétion éosinophile ainsi que des éléments phagocytaires ont été signalés. Le sperme n'a pas été trouvé. Chez un exemplaire (N° 1) les spermathèques faisaient complètement défaut.

Tableau VIII.

Protocoles des expériences avec *Eiseniella tetraedra f. typica* (Sav.).

Localité — Šárka (mare).

Individu No	Date de capture	Date d'isolation	Devenu sexuellement mûr	Nombre de cocons pondus	Nombre de cocons destinés au développement	Nombre de cocons aux embryons développés	Date de fixation du ver	Spermathèques
1	30. X. 31	31. X. 31	?	11	10	9	28. I. 32	Non développées
2	„	7. XI. 31	29. XII. 31	19	18	17	23. I. 52	Pas de sperme
3	„	„	19. XII. 31	10	10	7	28. I. 32	Pas de sperme
4	„	31. X. 31	?	9	9	9	12. III. 32	Pas de sperme
Nombre total de cocons:				49	47	42 (86 %)		

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V. EXPULSION DES GLOBULES POLAIRES CHEZ *LIMNODRILUS HOFFMEISTERI* CLAP.

Dans son travail sur le développement et la fécondation des œufs chez les Annelides E. GATHY (1900) indique que «chez le *Tubifex* les bâtonnets n'étant pas plus nombreux dans la première figure de segmentation que dans les figures d'expulsion des globules, il y a donc réduction de nucléïne et cette réduction n'a pu se faire qu'après l'expulsion du second globule au moment de la fécondation, ou pour employer le langage des botanistes, au moment de la germination de l'œuf» (p. 36).

Cette observation de E. GATHY sur la relation du nombre de chromosomes dans le premier et le second globule polaires d'un côté, et dans la première figure de segmentation de l'autre, a d'abord donné à L. ČERNOSVITOV (1927) l'idée de supposer, que chez *Tubifex tubifex* il existe une forme de parthénogénèse, semblable à celle qui avait été signalée par L. DONCASTER (1907) chez *Nematus ribesii* et par W. SCHLEIP (1910) chez *Rhodites rosae*. L'auteur a cru, que E. GAHTY avait été en présence des œufs non fertilisés. Pourtant les propres recherches de L. ČERNOSVITOV (l. c.) l'ont obligé de premier abord à renoncer à cette théorie. Pour expliquer la faculté de reproduction sans fécondation réciproque qu'il avait découverte chez *Tubifex tubifex*, l'auteur, comme je l'ai déjà indiqué ci-dessus, est porté à admettre l'existence de l'autofécondation. Il écrit: «Bei meinen in Serien unternommenen Untersuchungen der Anfangsstadien der Entwicklung und Bildung der Richtungskörper bei einer grossen Anzahl von Eiern, sowohl durch normale Individuen abgelegte, welche Spermatophoren in den Samentaschen aufwiesen, als auch durch Individuen ohne Samentaschen, oder welche ihre Genitalorgane im isolierten Zustande ausgebildet hatte, konnte ich feststellen, dass keinerlei Differenz in der Anzahl der Chromosomen bestand und daher eine parthenogenetische Entwicklung bei *Tubifex* nicht stattfand und wir es somit nur mit einer Selbstbefruchtung zu tun haben. — Ich bin auch in der Lage, die Angaben von E. GATHY bestätigen zu können, dass der erste und zweite Richtungskörper und die erste Teilungsfigur sowohl, als auch die von mir gezählten Figuren der Mikromerenbildung und der späteren Furchungsstadien die gleiche Anzahl von Chromosomen besitzen» (p. 592).

Contrairement à l'opinion de E. GATHY, selon laquelle ce nombre est de 110, L. ČERNOSVITOV n'a pu compter plus de 76 chromosomes.

De même que L. ČERNOSVITOV, pour expliquer la faculté des œufs de *Limnodrilus hoffmeisteri, L. claparedeianus, Rhynchelmis limosella* et

Eiseniella tetraedra de se développer sans fécondation réciproque, je dois admettre deux modalités probables: 1) parthénogénèse, 2) autofécondation.[1]

En ce qui concerne *Limnodrilus hoffmeisteri* j'ai tâché de trouver la solution du problème en étudiant, à l'exemple de L. Černosvitov, la relation entre le nombre de chromosomes dans les cinèses polaires et dans les figures de segmentation des œufs, pondus par les individus fécondés et non fécondés.

Je ne peux pas donner le tableau complet de la maturation et des premiers stades de segmentation. Mon matériel a été relativement peu nombreux de sorte que je n'ai pas pu observer plusieurs stades intermédiaires, indispensables à la reconstitution de la marche du processus.

1) Première cinèse polaire.

Chez *Limnodrilus hoffmeisteri,* de même que chez *Tubifex, Rhyacodrilus, Enchytraeidae* et *Rhynchelmis,* le fuseau de la première cinèse polaire (Pl. I, fig. 1) se constitue déjà bien avant la ponte, à l'époque où l'œuf se trouve encore dans l'ovisac. Nous y sommes déjà en présence de la métaphase typique de la première cinèse polaire.

Le fuseau est situé à une certaine distance de la membrane de l'œuf. Il est orienté tangentiellement à la membrane ou, plus souvent, forme avec elle un certain angle. Il mesure 41—43 μ de longueur, sa largeur étant 25,5 μ.

Chaque pôle de la figure est présenté par un assez grand (10,25 μ) centrosome[2] dont la centrosphère présente une structure légèrement réticulaire, dûe probablement à l'action des fixateurs. La centriole étant très petite il est assez difficile de la trouver surtout dans les œufs qui n'avaient pas quitté le corps du vers. L'astrosphère entourant le centrosome est formée de radiations irrégulières qui disparaissent entre les enclaves vitellines. Elle est moins typique que chez *Tubifex.*

Entre les pôles on observe un solide faisceau de fibrilles centrales plus sombres, qui portent des chromosomes formant une plaque équatoriale. Ces fibrilles centrales restent droites tandis que les fibrilles extérieures entourant le faisceau central sont recourbées et plus claires. Elles ne portent pas d'éléments chromatiques.

[1] Quant à *Eiseniella tetraedra* la possibilité de parthénogénèse paraît être très considérable compte tenu de ce fait que chez les individus examinés je n'ai trouvé que des stades peu avancés de spermatogénèse tandis que les spermatozoïdes mûrs faisaient défaut. N'ayant pas étudié ce problème d'une façon détaillée je ne peux pas affirmer que chez les individus en question les spermatozoïdes faisaient absolument défaut pendant la période de la ponte. De nouvelles expériences dans cette direction sont indispensables pour qu'on puisse faire des conclusion plus exactes.

[2] Pour désigner les différentes parties des pôles du fuseau je me sers de la terminologie adopté par W. Chimkewitch (1923). D'après cet auteur le corpuscule, situé au centre du pôle — la centriole — et la zone de protoplasme modifié qui l'entoure — la centrosphère, — forment ensemble le *centrosome,* entouré d'une couche de protoplasme radié — astrosphère.

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Fig. 2. Chromosomes de la plaque équatoriale de la première cinèse polaire avant la ponte.

Les chromosomes de la plaque équatoriale sont bivalents (diades) et de différentes formes (fig. 2). Une partie d'entre eux se présentent comme formés de deux bâtonnets s'appliquant sous un angle. Leurs extrémités libres sont éffilées (fig. 2, a, b, c, d). Ces chromosomes bivalents sont rangés, comme l'indique la fig. 2, en deux séries.[1] Chaque paire de chromosomes constitue un groupe très semblable à la tétrade. Il me parait pourtant impossible de désigner ces groupes par le terme en question, les vraies tetrades (chromosomes tétravalents) se formant à un stade plus avancé, par voie de division longitudinale des diades.

Une autre partie des chromosomes se présentent comme des éléments f-formes décrits par F. VEJDOVSKY et A. MRÁZEK (1903) chez *Rhyacodrilus coccineus* (= *Ilyodrilus coccineus*) et *Rhynchelmis limosella* et plus tard par F. VEJDOVSKY (1907) chez les *Enchytraeidae*. Ces éléments sont formés de deux bâtonnets juxtaposés (fig. 2, e, f, g) formant une ligne droite ou un angle. Certains chromosomes bivalents offrent l'aspect de bâtonnets s'entrecroisant (fig. 2, h) ou s'appliquant par leurs bouts dilatés (fig. 2, i).

On observe la métaphase encore pendant quelque temps après la ponte. Les chromosomes gonflent fortement et leurs dimensions grandissent. Quelques-uns d'entre eux restent bivalents (diades). D'un côté ce sont probablement les chromosomes modifiés a, b, c, d, de la fig. 2, dont les bouts se sont

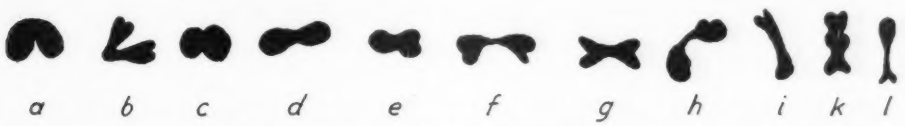

Fig. 3. Chromosomes de la plaque équatoriale de la première cinèse polaire après la ponte.

arrondis (fig. 3, a), de l'autre côté on peut les interpréter comme les f-chromosomes épaissis et devenus plus courts (fig. 3, c, d). D'autres chromosomes sont déjà tétravalents (tétrades). Déjà dans les œufs qui n'ont pas quitté les ovisacs, on trouve un certain nombre de f-chromosomes qui paraissent se

[1] Quelquefois les deux chromosomes, formant le groupe sont extrêmement rapprochés (fig. 2, b) et il parait que leur extrémités se sont fondues, ce qui rappelle beaucoup les diades signalées par F. VEJDOVSKY (1907) chez certains autres Oligochètes. J'ai été porté à interpréter chacun de ces chromosomes comme univalent et à envisager le groupe entier comme diade. Je n'ai pas étudié le processus de formation de ces chromosomes. Mais le nombre de chromosomes comptés sur les coupes sagittales des œufs non éliminés n'a pas coïncidé avec celui signalé dans la plaque équatoriale des œufs pondus, où les chromosomes sont plus faciles à compter, que si je les interprétais comme bivalents (diades).

diviser longitudinalement (fig. 2, k, l). La formation des tétrades commence donc avant la ponte. Après le passage de l'œuf dans le cocon elle accelère seulement sa marche. F. VEJDOVSKY (1907) décrit un phénomène semblable chez les *Enchytracidae* et *Rhynchelmis*. Les chromosomes tétravalents e, f, g, h, i, k, l représentés sur la fig. 3, se sont probablement formés par voie de division longitudinale des chromosomes c et d. On peut donc les déduire des f-chromosomes, qu'on observe dans l'ovule encore non éliminé. Le chromosome tétravalent b (fig. 3) provient, peut-être, du chromosome a (fig. 3) quoiqu'on puisse aussi le déduire du chromosome g (fig. 2).

Il est très difficile de compter les chromosomes de la plaque équatoriale d'un ovule qui n'a pas encore quitté l'ovisac, puisque leur forme et leurs dimensions sont extrêmement variables. Leur nombre établi sur les coupes transversales de la plaque équatoriale a été toujours un peu plus grand chez les ovules dans les ovisacs que chez les œufs pondus. Ce fait est dû, on peut le croire, à ce que les longues f-chromosomes se trouvent sur les deux coupes

Fig. 4. Chromosomes de l'anaphase de la première cinèse polaire.

successive. Il est beaucoup plus facile de compter les chromosomes raccourcis et arrondis qui forment la plaque équtoriale de l'œuf pondu.

J'ai signalé ici la présence de 92 chromosomes dont quelques-uns sont bivalents tandis que les autres se présentent déjà comme tétravalents.

Après la ponte le fuseau de la première cinèse polaire grandit ($80 \times 30 - 44\ \mu$) et s'approche de la membrane de l'œuf s'orientant perpendiculairement à celle-ci. En même temps le nombre de chromosomes redouble (184). Pendant quelque temps les chromosomes restent répartis sans ordre dans tout le fuseau soit dans le sens de sa longueur, soit dans le sens perpendiculaire ou, enfin, formant avec l'axe un certain angle. A ce stade ils présentent, comme on le voit sur la fig. 4, le type bivalent (diades) ou tétravalent (tétrades encore non partagées en diades). Dans le fuseau les fibrilles périphériques et centrales ne se laissent plus distinguer. La fig. 2 (pl. I) présente un stade plus avancé, les chromosomes définitivement partagés en diades forment deux rangs des deux côtés du plan équatorial du fuseau. A ce stade, en tant qu'il a été possible de l'observer, les deux centrioles commencent à disparaître. Sur la fig. 3 (pl. I), où on voit déjà le pôle externe du fuseau faire saillie en forme de protubérance à la surface de l'œuf, les centrosomes ne se laissent plus voir. Les chromosomes se trouvent dans la proximité immédiate de chacun des pôles. La fig. 4 (pl. I) présente une protubérance déjà entièrement formée qui renferme l'astre externe de la figure caryocinétique. J'ai

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compté dans chacun des astres de ce stade 92 chromosomes bivalents dont les bouts libres sont orientés vers le centre de la figure.

Chez *Limnodrilus hoffmeisteri* on observe donc au cours de la formation du premier globule polaire la disparition des deux pôles du fuseau. Cette espèce en diffère de *Tubifex* chez lequel d'après E. GATHY le pôle interne persiste.

Quant au sort de la centriole du pôle externe, E. GATHY admet, en ce qui concerne *Tubifex*, deux possibilités: ou (ce qui est plus probable) elle est expulsée avec le premeir globule polaire, ou elle pénètre dans l'œuf tout en devenant inactive. Il est évident qu'on peut faire les mêmes suppositions en ce qui concerne la centriole du pôle externe de *Limnodrilus hoffmeisteri*, le pôle interne seul se présentant ici au cours de la formation du fuseau de la seconde figure de maturation. Sa centriole correspond visiblement à celle de la

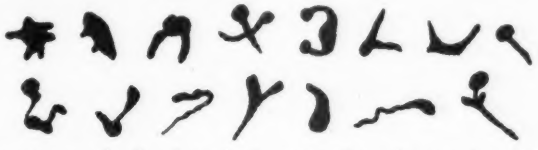

Fig. 5. Chromosomes de l'œuf après la separation du premier globule polaire.

centrosome interne de la première cinèse polaire, qui est resté pendant quelque temps à l'état inactif.

Chez *Limnodrilus hoffmeisteri* le premier globule polaire se détache de la même maniere que chez *Tubifex*. Sur les fibrilles du fuseau on voit apparaître des granulations formant une ligne au niveau de la membrane ovaire («plaque cellulaire»). Le globule polaire se détache ensuite suivant cette ligne.

Encore avant la séparation du globule polaire dont les chromosomes bivalents restent jusqu'au moment de dégénérescence amassés dans un seul endroit et ne reconstituent jamais de noyau, les chromosomes restés dans l'œuf subissent certains changements de forme. Ils sont souvent un peu plus volumineux que ceux du globule polaire et se présentent, eux aussi, comme bivalents (diades). La fig. 5 fait voir les différentes formes des ces chromosomes. Autour de chacun d'entre eux il se délimite une vacuole achromatique (Pl. I, fig. 5). L'aspect général fait croire à la reconstitution du noyau.[1]

[1] J'ai cru d'abord être en présence de la formation des caryomères après l'expulsion du second globule polaire, puisque le tableau général rappelait beaucoup les phénomènes, décrits par F. VEJDOVSKY (1907) che *Rhynchelmis*. Pourtant dans ces cas, même sur d'assez bonnes préparations je n'ai pu trouver qu'un seul globule polaire. En outre je n'ai jamais observé le second globule polaire au noyau non reconstruit, tandis qu'ici au moment, où dans l'œuf se forment de petites vacuoles semblables aux caryomères, le globule polaire, encore non détaché, présente des chromosomes qui n'ont éprouvé aucun changement. Ils ont donc le même caractère que les chromosomes du premier globule polaire. Sur d'autres préparations j'ai reussi à constater que le noyau du second globule polaire se forme à la même époque et de la même manière que celui de l'œuf (pl. II, fig. 10, 11). A ce moment le second globule ne s'est pas encore détaché. Quand ce phénomène s'effectue, le globule présente déjà des caryomères volumineux.

Pourtant la dislocation complète des chromosomes en caryomères, qu'on observe après l'expulsion du deuxième globule polaire, autant que nous ayons pu le constater, ne se laisse pas voir. En tout cas je n'ai pas observé de stades qui auraient prouvé le contraire. Cet état de chromosomes, qu'on pourrait désigner comme «pseudoreconstruction», n'est pas, on peut le croire, sans importance dans le processus d'échange de matières entre les éléments chromatiques et cytoplasmiques de l'œuf avant le commencement de la nouvelle cinèse polaire. F. Vejdovsky (1907) étudiant un stade analogue chez *Rhynchelmis limosella* a été visiblement en présence du même phénomène. Il croit pourtant que tous ces changements sont dûs à l'action des fixateurs. Cet auteur écrit: «Es ist nunmehr notwendig noch auf eine Eigentümlichkeit der Tochterdyaden hinzuweisen. In manchen Eiern nämlich, die gehörig fixiert worden waren oder nach einer raschen Behandlung mit Alkohol findet man die Tochterdyaden stark geschrumpft, in der Gestalt von Kügelchen, die immer von einem hyalinen Höfchen umgeben sind. Die letzteren erinnern nun an eine Karyomerenbildung der zweiten Reifungsteilung, tatsächlich aber stellen sie in der Anaphase der 1. Teilung Artefakte vor, welche an den fixierten oder sonst behandelten Präparaten gar nicht zum Vorschein kommen» (p. 48). Je ne peux pas admettre que tous les phénomènes signalés chez *Limnodrilus* et cités ci-dessus soient dûs à l'action des fixateurs. Je n'ai jamais observé rien de semblable aux autres stades, bien que tous les œufs aient été fixés avec le même liquide. E. Gathy ne décrit pas ces phénomènes chez *Tubifex*.

Le premier globule polaire se détache quand l'œuf est au stade de «pseudoreconstruction». Je n'ai jamais vu la bipartition ultérieure du globule. Ce n'est que dans un seul cas que j'ai pu observer un tableau rappelant dans une certaine mesure cette bipartition mais aucune doute n'est possible sur le caractère anomal de ce phénomène. Dans un cocon pondu par un individu fertilisé, deux œufs ont déjà expulsé les deux globules polaires. Dans l'un d'entre eux (1 autre était endommagé) on peut voir des caryomères typiques. Le troisième ovule présente l'anomalie en question (pl. I, fig. 9). Près du pôle interne de sa figure caryocinétique on distingue de petits chromosomes peu nets, non modifiés, en caryomères, chromosomes qui correspondent à ceux de la seconde cinèse polaire. Au bout externe du fuseau est rattaché un globule polaire composé de deux parties inégales réunies par un fin cordon. D'après son aspect le globule en question doit être interpreté comme premier globule polaire. Les deux parties renferment de petits chromosomes peu nets dont le nombre total égale à peu près le chiffre que nous avons établi (92). Nous sommes sans doute en présence d'un cas de maturation retardée d'un ovule arrêté au stade d'expulsion du premier globule polaire. Ce dernier sans se détacher de l'ovule est en train de s'etrangler ce qui rappelle beaucoup la bipartition et se présente comme un processus, dû certainement à la marche anormale de la maturation.

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A la fin du processus d'expulsion du premier globule polaire la membrane de l'œuf, très mince jusqu'à ce moment, commence à s'apaissir. Ses couches externes se délaminent souvent de l'œuf.

2) Deuxième cinèse polaire.

Je n'ai qu'une seule préparation présentant le stade intermédiaire entre la «pseudoreconstruction» et celle de la plaque équatoriale de la deuxième cinèse polaire.

Cette préparation montre que le fuseau de la seconde figure de maturation en voie de formation, présente au pôle interne un centrosome typique, muni d'une centriole très distincte (pl. I, fig. 6). Ce centrosome a dû se former ici de nouveau, puisque chez *Limnodrilus hoffmeisteri,* contrairement à ce qu'on observe chez *Tubifex* (d'après E. GATHY chez ce ver le pôle interne

Fig. 6. Chromosomes au commencement de la deuxième cinèse polaire.

de la première cinèse «persiste dans son integrité»), les deux pôles disparaîssent encore avant la séparation du premier globule polaire. Ce centrosome de forme typique ne persiste pourtant que peu de temps, pendant que les chromosomes en forme de diade et de tétrades (fig. 6) déjà exempts de vacuoles achromatiques commencent à former la plaque équatoriale de la deuxième cinèse polaire. Un fuseau, entièrement constitué portant des chromosomes réunis en plaque équatoriale ne présente plus de pôle interne typique (pl. I, figs. 7, 8). Dans certains cas il serait encore possible de parler d'un centrosome, mais chez la plupart des figures nous ne trouvons à sa place qu'une dense formation réticulée à laquelle se rattachent les fibrilles de fuseau. Je n'ai pas pu déceler avec certitude la présence de la centriole. Le bout extérieur du fuseau, dont les fibrilles sont souvent relativement épaisses est formé à ce stade de rayons s'entrelaçant en réseau. A l'endroit où ils atteignent la membrane, celle-ci présente une petite excavation. Le fuseau de la seconde cinèse polaire mesure à peu près 57—67 μ de longueur, sa largeur étant 32—33 μ.

La plaque équatoriale de la seconde figure de maturation (pl. I, fig. 7) est formée de chromosomes bivalents (diades) et tétravalents (tétrades) assez irrégulièrement répartis. Le nombre de chromosomes dans cette plaque équatoriale est le même que dans la plaque de la première cinèse polaire — c'est-à-dire 92.

Ces chromosomes (fig. 7) se dédoublent, comme on peut le voir, par la même voie de division longitudinale, qu'on observe au cours de la première cinèse, et forment ensuite deux asters des deux côtés de l'équateur du fuseau.

Fig. 7. Chromosomes de la plaque équatoriale de la seconde cinèse polaire.

Ce stade de diaster est représenté sur la fig. 8, pl. I. Chaque aster se compose de 92 chromosomes bivalents.

Je n'ai pas observé de stades intermédiaires entre le diaster et le moment que représente la fig. 10, pl. II. Je ne puis donc me prononcer sur l'origine de la protubérance, dans laquelle passe le bout externe de la seconde cinèse polaire[1], ni sur la transformation des chromosomes en caryomères en forme des vésicules acidophiles. Ces caryomères se forment, comme on le voit sur la fig. 10, pl. II, simultanément dans l'ovule et dans le second globule polaire. On peut croire que ce processus s'effectue de même façon que chez *Rhynchelmis* où il est décrit par F. VEJDOVSKY. Chaque caryomère initial serait donc issu d'un chromosome bivalent.

De même que chez *Tubifex* (E. GATHY, 1900) les caryomères se fondent entre eux de sorte que leur nombre diminue. Nous ne trouvons bientôt que quelques volumineux caryomères secondaires qui s'appliquent les uns contre les autres. Fig. 11, pl. II représente le stade, où les deux gros caryomères, formés par la fusion des caryomères initiaux, sont prêts à reconstituer le noyau définitif. Il me parait impossible d'interpréter un d'entre eux comme pronucleus mâle, l'autre comme élément femelle, puisque nous trouvons la même paire de caryomères, qoiqu'un peu moins volumineux, aussi dans le globule polaire.

Dans le second globule polaire je n'ai jamais observé de chromosomes d'aspect ordinaire, typiques pour le premier globule, comme N. GATHY l'avait quelquefois observé chez *Tubifex tubifex*. Le second globule polaire reconstruit toujours son noyau. Son volume est ordinairement le même ou un peu plus petit que celui du premier (30—31 μ). Les enclaves de vitellus si elles ne font pas défaut, sont peu nombreuses. Sur la fig. 16 (pl. II) on voit une représentation parallèle des deux globules polaires expulsés par le même ovule (sur la préparation ces globules se trouvent côte à côte).

3) Première figure de segmentation.

La fusion graduelle des caryomères aboutit à la formation du noyau qui doit être envisagé (nous verrons ci-dessus pourquoi) comme noyau de segmentation.

Ce noyau s'éloigne de la membrane, emportant avec lui à une certaine distance l'amas de cytoplasme réticulé qui persiste comme résidu de la seconde cinèse polaire. On y voit apparaître de nombreux nucléoles (pl. II, figs. 11,

[1] Ce processus correspond probablement à la formation de la protubérance de la première cinèse polaire représentée sur les figs. 3 et 4 (pl. I).

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12). Le noyau se présentant sous la forme de vésicule assez volumineuse, entourée d'une couche de cytoplasme périnucléaire, reste pendant un court délai de temps (jusqu'au moment de la formation de la première figure de segmentation) inactif. Il renferme du caryoplasme transparent. Les éléments chromatiques en forme de grains irrégulièrement répartis sont amassés sous la membrane nucléaire.

Quant à la formation de la première figure de segmentation je n'en peux dire que bien peu de choses. Mes observations concernant ce sujet sont très accidentelles et l'absence de toute une série de stades intermédiaires ne me permet que d'esquisser le processus en ses grandes lignes.

Bientôt à côté du noyau inactif il apparaît un centrosome présentant une centriole marquée et entouré d'astrosphère (pl. II, fig. 13). Les nucléoles commencent à prendre les colorants plasmatiques. Bientôt ils disparaîssent. Entre le centrosome et le noyau se fait voir un cône de radiations («cône polaire» de G. PLATNER, 1889), qui repousse graduellement à l'interieur la

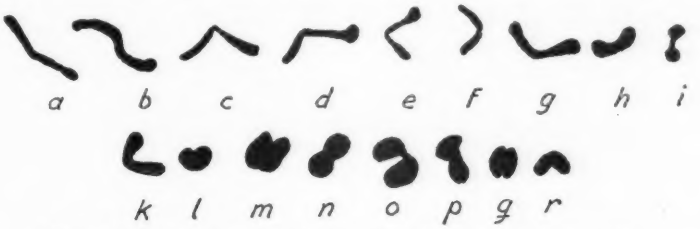

Fig. 8. Chromosomes de la première figure de segmentation.

membrane nucléaire. En même temps le noyau s'étire dans la direction perpendiculaire aux rayons du cône et devient vacuolisé (pl. II, fig. 13).

Je ne peux pas dire comment les grains de chromatine se transforment en chromosomes. En tout cas les chromosomes se constituent dans le noyau à l'époque où celui-ci présente encore une membrane quoique devenue très pâle. On observe aussi à ce moment un seul centrosome. Les chromosomes ont leur aspect initial — celui de petits bâtonnets étirés ou recourbés (fig. 8, a, b). On ne peut pas établir avec certitude s'ils sont bivalents, quoique cela semble très probable. Aux stades plus avancés ils sont formés de deux bâtonnets juxtaposés et formant un angle. Leur caractère bivalent est évident (fig. 8, c—k). Quelques-uns d'entre eux se sont fortement raccourcis (fig. 8, i).

La membrane nucléaire se dissout de plus en plus et enfin disparaît rendant libres les chromosomes, fortement raccourcis et arrondis de type bivalent (fig. 8, k—r), qu'on observe à l'extrémité du cône polaire. Ils forment un rang relativement régulier (pl. II, fig. 14).

Je n'ai pas reussi à établir, à quel moment et de quelle manière apparaît la deuxième centriole qui forme le second centrosome de la première figure de

segmentation. On peut croire qu'elle est dûe à la bipartation de la première, ce processus s'effectuant immédiatement après la disparition de la membrane nucléaire.

Le fuseau entièrement constitué de la première figure de segmentation (pl. II, fig. 15) présente deux pôles typiques, aux centres desquels on voit distinctement des centrioles. De puissantes astrosphères entourent les centrosomes. Contrairement à ce qu'on observe dans le fuseau de la première cinèse polaire, celui de la première figure de segmentation ne présente pas de différence entre les fibrilles centrales et périphériques. Les fils périphériques, eux aussi, atteignent la plaque équatoriale. La première figure de segmentation est beaucoup plus grande que les cinèses polaires. Elle mesure 158 μ de longueur, la largeur étant 39,5 μ. Chaque pôle mesure à peu près 20 μ.

Je n'ai pas eu de préparation qui put permettre de compter précisement les chromosomes de la plaque équatoriale, déjà formée, de la première figure de segmentation. Sur une coupe sagittale représentée sur la fig. 15, pl. II, il est très difficile d'effectuer cette opération. J'ai établi le nombre de chromosomes de la première figure de segmentation d'après quelques préparations qui les présentaient encore irrégulièrement répartis à l'intérieur du noyau la membrane nucléaire étant intacte. J'ai contrôlé ensuite mes constatations d'après les préparations qui présentaient les chromosomes en forme de diades formant un rang à la base du cône polaire. Autant que j'aie pu l'établir le nombre de chromosomes dans la plaque équatoriale formée, correspond à ce que j'ai signalé ici.

Dans la première figure de segmentation le nombre de chromosomes est le même que dans la plaque équatoriale de la première et de la seconde cinèses polaires (92).

Aux stades plus avancés de segmentation, j'ai signalé dans les figures caryocinétiques à peu près le même nombre de chromosomes.

Tous les processus de formation des globules polaires ainsi que de la première figure de segmentation, décrits ci-dessus, sont caractéristiques pour les œufs pondus par les exemplaires fécondés de *Limnodrilus hoffmeisteri* aussi bien que pour les œufs non fertilisés par le sperme d'un autre individu. Aucune différence entre ces deux catégories d'œufs ne se laisse signaler.

Dans les deux cas la maturation de l'ovule, est accompagnée de l'expulsion de deux globules polaires et la plaque équatoriale des cinèses polaires, de la première figure de segmentation ainsi que des figures suivantes renferme toujours le même nombre de chromosomes (92).

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4) Conclusions.

Le résultat que j'ai obtenus concorde complètement avec les constatations de L. Černosvitov (1927) concernant *Tubifex tubifex*.

Nous avons vu que L. Černosvitov se basant sur ses observations avait reconnu l'existence de l'autofécondation chez *Tubifex*. Néanmoins je ne peux pas affirmer que nos résultats excluent définitivement la seconde supposition possible — celle de parthénogénèse.

Nous avons vu que chez *Limnodrilus*, de même que chez *Tubifex*, au cours de l'expulsion des globules polaires il ne se produit pas de réduction du nombre de chromosomes. F. Vejdovsky (1907) a signalé le même phénomène chez les *Enchytraeides* et chez *Rhynchelmis*. Cet auteur émet l'hypothèse, selon laquelle la réduction numérique des chromosomes par voie de copulation s'effectue pendant la maturation des ovules, quand ceux-ci sont au stade de synaptocytes. D'après F. Vejdovsky «die gepaarten Chromosomen verschmelzen der Länge nach und führen zur Reduktion der Chromosomen auf die Hälfte» (p. 69). Cette hypothèse est pourtant inapplicable à *Tubifex* et à *Limnodrilus*, le nombre de chromosomes bivalents étant ici le même au cours des cinèses polaires que dans la première figure de segmentation.

L'hypothèse, d'après laquelle le spermatozoïde pénétrant dans l'ovule ne joue chez ces espèces que le rôle d'agent stimulant la segmentation et ne prend pas part à l'amphimixie (mérospermie) comme cela a été constaté chez *Rhabditis aberrans* (E. Krüger, 1913) et chez *Rhabditis anomala* (P. Hertwig, 1922) à l'heure actuelle ne peut pas être solidement basée.

Nous sommes donc obligés de nous arrêter sur la théorie émise par E. Gathy et citée ci-dessus, selon laquelle la réduction du nombre de chromosomes s'effectue après l'expulsion du second globule polaire au moment de la fertilisation sensu stricto (germination).

Mais, si la réduction du nombre de chromosomes s'effectue après l'expulsion des globules polaires, mes résultats concernant *Limnodrilus* et ceux, que L. Černosvitov (1927) avait obtenus chez *Tubifex*, ne peuvent pas donner la solution du problème qui nous intéresse. Égalité de nombres de chromosomes dans les cinèses polaires et dans la première figure de segmentation des œufs pondus par les individus fécondés et non fécondés est de ce point de vue sans importance. On peut croire que:

1) Si l'œuf est fécondé, le nombre de ses chromosomes, réduit au moment d'amphimixie, est ensuite suppléé par les chromosomes du spermatozoïde.

2) Si l'œuf n'est pas fertilisé, la réduction du nombre de chromosomes n'a pas lieu et le développement doit s'effectuer dans ce cas par voie de parthénogénèse.

Dans les deux cas le nombre de chromosomes dans la première figure de

segmentation doit être égal à celui de chromosomes dans les plaques équatoriales des globules polaires.

On peut en déduire qu'il n'est possible d'obtenir la solution du problème qu'en appliquant une autre méthode.

Celle-ci, dont parmi les autres parle L. Černosvitov (l. c.) offre une trop grande possibilité d'erreur. L. Černosvitov indique que: «Anderseits kann auch die Tatsache als Beweis dienen, dass nur wenige von isolierten Individuen abgelegte Kokons in der Weiterentwicklung versagten. Zu Ende der Sexualtätigkeit der *Tubifex* findet die Reduktion der Hoden früher statt als die der Eierstöcke, wobei die männlichen Sexualbestandteile durch Lymphocyten vernichtet werden. Man kann Individuen mit einer Anzahl von Eiern, doch ohne Sperma, in den Samensäcken beobachten, wobei sich von einer Tendenz zur Proterandrie sprechen liesse, die jedoch nicht deutlich zum Ausdruck gelangt. Solche unentwickelte Kokons können von Individuen abgelegt werden, die schon kein Sperma in den Samensäcken aufweisen und die Feststellung auch dieses Faktums kann zum Beweise einen Selbstbefruchtung bei *Tubifex* dienen. Trotz meiner vielen Versuche gelang mir bisher diese Feststellung nicht, da ich nur eine geringe Anzahl nichtentwecklungsfähiger Kokons besass» (p. 593).

Quand on isole de pareils individus (assez rares), chez lesquels les testicules font défaut et les vésicules séminales semblent ne pas présenter de sperme, on ne peut quand même pas être sûr que les vésicules et la cavité du corps soient réellement exempts de spermatozoïdes.

J'ai eu l'occasion d'isoler trois pareils individus de *Tubifex tubifex*. Examinés in vivo ils ne présentaient ni testicules, ni spermathèques, ni sperme dans les vésicules séminales pas plus que dans la cavité du X^{e} segment. Le premier individu a déposé 4 cocons, dont j'ai disloqué un par hasard et les autres ont achevé leur développement. Le ver a été fixé immédiatement après l'élimination du dernier cocon (qui avait donné l'embryon) et sur les préparations je n'ai pas effectivement trouvé de sperme dans les vésicules. Un autre exemplaire a pondu 13 cocons, dont l'un fut aussi disloqué et les autres achevèrent leur développement. L'individu en question a été fixé quelque temps après la ponte du dernier cocon (qui s'est développé). D'après les préparations les vésicules n'ont pas renfermé de spermatozoïdes. Le troisième exemplaire a pondu un seul cocon, dans lequel les œufs se sont développés. Ce ver a été fixé aussi peu de temps après et la préparation, soumise à un examen très attentif, fit voir des spermatozoïdes parmi les lymphocytes. Je n'attribue donc aucune importance aux résultats obtenus chez les deux premièrs vers qui sembleraient parler en faveur de la parthénogénèse et je ne les cite ici que pour souligner qu'une pareille méthode est extrêmement précaire.

Je crois que la constatation des résidus de spermatozoïdes ou du pronucleus mâle dans les œufs pondus par les individue non fécondés, où la présence

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des spermatozoïdes dans leurs cocons, seules pourraient servir de preuves indiscutables en faveur de l'autofécondation.

Il est pourtant extrêmement difficile de faire les observations en question, puisque chez les Limicoles les spermatozoïdes, contrairement à ce qu'on observe chez certains Terricoles, ne subsistent dans le cocon sans doute que bien peu de temps. F. VEJDOVSKY (1888—92) et, plus tard, lui et A. MRÁZEK (1903) n'ont jamais trouvé de spermatozoïdes dans les cocons de *Rhynchelmis limosella*. Ce n'est que dans les œufs qu'ils se faisaient voir. De même ni E. GATHY (1900), ni A. PENNERS (1922), ni L. ČERNOSVITOV (1927) n'ont réussi à déceler la présence des spermatozoïdes dans les cocons de *Tubifex tubifex*, récemment pondus. Les tentatives de A. DITLEVSEN (1904) portant sur *Lumbricillus lineatus* (= *Pachydrilus rivalis*) et de J. DELPHY (1920, 1920 a, v. aussi 1921), qui avait choisi comme objet *Clittelio* aboutirent au même résultat négatif.

Quant à moi, je n'ai pas réussi non plus à trouver les spermatozoïdes ni dans les cocons pondus par les individus fécondés, ni dans les cocons, éliminés par les exemplaires isolés encore avant leur maturité sexuelle.

En ce qui concerne les spermatozoïdes, pénétrés dans l'œuf, et le pronucleus mâle, mon resultat est jusqu'à présent nul aussi. Ni dans les œufs fécondés, ni dans les œufs, pondus sans copulation croisée, je n'ai jamais observé rien de ce qui aurait pu être interprété, sans aucune doute, comme spermatozoïde ou pronucleus mâle.

Quant aux zones, signalées par E. GATHY (voir la citation ci-dessus) ce n'est que dans un seul cas que j'ai pu observer quelque chose de semblable dans un œuf pondu par un individu isolé. Sur la fig. 17 (pl. II) nous voyons une grande zone de ce type (à gauche) dans la proximité des chromosomes de la seconde cinèse polaire, dispersés dans le résidu du cordon cytoplasmique du fuseau, ainsi que deux plus petites zones (à droite). Si les zones en question sont réellement dûes aux spermatozoïdes pénétrés dans l'œuf, comme E. GATHY le suppose, leur nombre témoignerait en faveur de la polyspermie. Je ne vois pourtant aucune raison permettant de les interpréter comme dérivés des spermatozoïdes. Malgré des observations minutieuses je n'ai pas réussi à constater dans les zones en question aucun résidu de spermatozoïdes. De petits points noirs dispersés dans le cytoplasme réticuleux de la grande zone, que j'ai pris d'abord pour des chromosomes mâles, ne sont en réalité, autant que j'aie pu m'en convaincre, que des éléments cytoplasmiques. Nous ne sommes pourtant pas autorisés à considérer ce résultat négatif comme un témoignage contre la supposition de E. GATHY, puisque de très petits chromosomes issus du noyau du spermatozoïde et le noyau même, si celui-ci reste intact en forme d'une petite caryomère, peuvent facilement échapper à la vue s'égarant entre les granulations mentionnées ci-dessus et les formations réticuleuses du cytoplasme.

Comme je l'ai dit ci-dessus, je suis obligé actuellement interprêter le noyau qui se constitue après l'expulsion du second globule polaire comme noyau de segmentation. A l'heure actuelle je ne puis que m'associer à l'opinion, selon laquelle le petit pronucleus mâle se mèle aux caryomères de l'œuf et se fond avec eux au moment de la constitution du noyau définitif. L'autre interprétation possible n'est pourtant pas exclue. Peut-être le noyau qui se constitue après l'expulsion du second globule polaire doit être considéré comme pronucleus femelle. Mais cette opinion admise, il faut supposer que la fusion des pronucleus s'effectue extrêmement vite.

E. GATHY (1900), lui non plus, n'a pu trouver de spermatozoïdes dans les œufs fécondés de *Tubifex*. Il écrit: «Nous n'avons pu suivre dans l'œuf le spermatozoïde, qui est très petit. Nous avons observé dans les œufs après l'expulsion du second globule, des zones, dûes vraisemblablement aux spermatozoïdes, où le protoplasme change complètement d'aspect: les enclaves y disparaissent, le reticulum y est très fin, mais nous n'avons jamais vu les radiations, dont s'entoure généralement le spermatozoïde en entrant dans l'œuf, et nous n'avons pas pu le déceler dès son entrée dans l'œuf des *Tubifex*, sans doute à cause de sa petitesse. D'un autre côté, si nous supposons que le noyau mâle se trouve au milieu de ces amas de vésicules que l'on observe quand le noyau tarde à se reconstituer, on comprend qu'il passe inaperçu» (p. 33).

E. GATHY parle ensuite des pronuclei mâle et femelle qu'il avait observés avant la constitution de la première figure de segmentation. L'auteur dessine à côté des pronucleus deux centrosomes entourés de centrosphères. Ces pôles commencent à peine à s'indiquer. Néanmoins nous ne devons admettre qu'avec beaucoup de réserve l'indication de E. GATHY concernant le pronucleus mâle puisque l'auteur, lui même, dit que le retardement de la fusion des caryomères n'est pas rare chez *Tubifex*.

L. ČERNOSVITOV (1927) non plus n'a pas eu de chance de déceler dans les œufs de *Tubifex tubifex* le spermatozoïde ou le pronucleus mâle, quoiqu'il examinât un grand nombre d'œufs, pondus par des individus fécondés et non fécondés.

A l'heure actuelle le problème de fécondation et du sort du spermatozoïde, pénétré dans l'œuf, chez les *Tubificidae* est donc loin d'être élucidé. En raison de cela la question qui nous intéresse — faut-il expliquer la faculté de se reproduire sans fécondation réciproque, propre à plusieurs espèces de cette famille, par l'autofécondation ou par la parthénogénèse — elle aussi, reste encore ouverte.

Il en est de même avec *Rhynchelmis limosella* et *Eiseniella tetraedra*. Je n'ai pas étudié leurs œufs du point de vue cytologique quoique la possibilité d'obtenir ici des résultats plus nets y soit beaucoup plus grande que chez les *Tubificidae*.

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5) Possibles mécanismes d'autofécondation chez les Oligochètes.

J'ai décrit ci-dessus, comment l'autocopulation s'effectue chez *Limnodrilus udekemianus.*

L'existence de ce phénomène chez *L. udekemianus* et son absence chez *L. hoffmeisteri* et *L. claparedeianus* quoique la situation des orifices génitaux y reste la même, est dûe, parait-il, à la différence de longueur des organes copulatifs de ces vers. Le court penis de *L. udekemianus* ne dépassant généralement 180 μ est, selon H. Ude (1929), seulement 4 fois plus long que large. Il peut-être sans doute, facilement introduit dans l'orifice de la spermathèque, quand le corps se recourbe à l'endroit situé entre la région de spermathèques et celle d'organes copulatifs. Les organes copulatifs de *L. hoffmeisteri* et de *L. claparedeianus* sont beaucoup plus longs. Chez la première espèce leur longueur (540—560 μ, d'après H. Ude 414 μ) dépasse selon cet auteur 11—12 fois la largeur. Les bouts distales sont légèrement recourbés. Chez *L. claparedeianus* les organes copulatifs atteignent 1500—1560 μ (1066 μ d'après H. Ude). Leur longueur dépasse 23—31 fois la largeur de la partie basale. Il est évident que, grâce à la longueur considérable des organes copulatifs, ces espèces — *L. hoffmeisteri* et *L. claparedeianus* — ne peuvent pas les introduire dans les orifices des spermathèques en recourbant le corps à l'exemple de *L. udekemianus.*

Si la faculté de *L. hoffmeisteri* et *L. claparedeianus* de se reproduire sans fécondation croisée est dûe à l'autofécondation, ce qui parait très probable, si l'on prend en considération l'existence de ce phénomène chez l'espèce voisine — *L. udekemianus,* — on peut faire les suivantes suppositions sur le mécanisme du processus en question:

1. C'est un processus interne qui se produit:
   a) par voie de pénétration active des spermatozoïdes à travers les parois des sacs séminaux et les dissépiments dans les ovisacs, où s'effectue la maturation des ovules.
   b) grâce à la pénétration des spermatozoïdes dans les ovisacs par les orifices qui, peut-être, existent dans les dissépiments comme cela à été constaté chez *Lumbriculus variegatus* (P. Ivanov, 1903), *Pheretima posthuma* (K. Bahl, 1919) etc. (v. chez J. Stephenson, 1930, p. 53—54).

2. Ou bien c'est un processus externe dû à l'éjaculation du sperme dans le cocon formé autour les segments génitaux qui se produit au moment de la ponte.

Ainsi que nous l'avons indiqué dans les pages qui précèdent L. Černosvitov (1927) admet à peu près les mêmes possibilités pour *Tubifex tubifex.*

Il faut les admettre aussi pour *Enchytraeus albidus* et *Rhynchelmis limosella* si chez ces espèces les premiers stades de segmentation sont aussi déterminés par l'autofécondation.

Dans ma communication préliminaire (1931) j'ai été plutôt porté à croire, que chez *Limnodrilus hoffmeisteri* et *L. claparedeianus* la seconde possibilité — processus externe — est plus probable. Je n'ai pu pourtant donner que des preuves indirectes en faveur de cette opinion — l'existence de l'autofécondation dûe à l'éjaculation du sperme dans les spermathèques chez *L. udekemianus* et le pourcentage relativement faible des cocons développés chez les individus isolés de *L. hoffmeisteri* et *L. claparedeianus* tandis que chez *L. udekemianus* dans les mêmes conditions il était beaucoup plus élevé. J'ai indiqué que ce faible pourcentage peut être expliqué ou par l'influence des facteurs ambiants ou par le fait, que les œufs ne sont fertilisés que dans les cocons, qui avaient reçu des spermatozoïdes éjaculés. Dans les cas, où, comme je l'ai cru d'abord, le sperme est éjaculé à chaque ponte, tous les cocons se développent. Aucun d'entre eux ne se développe si l'éjaculation n'a pas eu lieu.

J'ai fait les conclusions exposées ci-dessus, me basant sur les observations faites avec les cocons, que j'avais ouverts assez longtemps après la ponte. Ils avaient donc eu le temps de parcourir tous les stades d'évolution et renfermaient, s'ils n'étaient pas pourris, déjà de jeunes vers.

Au cours de mes recherches cytologiques je n'ai pourtant jamais observé de cocons, récemment pondus par des exemplaires isolés, qui renfermaient des œufs non segmentés commençant à pourrir. Ils présentaient toujours ou de différents stades d'élimination de globules polaires ou les premiers stades de segmentation. Cette circonstance prouve que mes assertions précédentes étaient éronnées. Chez *L. hoffmeisteri* et *L. claparedeianus* le pourcentage des œufs développés sans fécondation réciproque est donc beaucoup plus élévé, que je l'ai d'abord supposé.[1] Au cours de mes premières expériences le pourcentage d'embryons développés a été pourtant assez bas — beaucoup plus bas que chez *L. udekemianus*. On peut expliquer ce phénomène par le fait que les embryons de *L. hoffmeisteri* et *L. claparedeianus* (peut-être seulement en cas d'autofécondation) sont plus sensibles à l'action de différents facteurs défavorables, de sorte que souvent leur développement s'interrompt.

On peut donc dire que chez *L. hoffmeisteri* et *L. claparedeianus* ainsi que chez les autres Limicoles, mentionnés ci-dessus, les deux modalités possibles — l'autofécondation interne et externe — sont à peu près également vraisemblables.[2]

Le processus d'autofécondation interne devrait être en réalité semblable au phénomène signalé par L. Cognetti de Martiis (1910, 1910 a) chez

[1] Il peut atteindre presque 100 %.

[2] Peut-être la probabilité de l'autofécondation externe est un peu plus grande grâce à l'existence de l'autofécondation, dûe à l'éjaculation du sperme dans les spermathèques chez *L. udekemianus*.

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Pareudrilus pallidus au cours de la fécondation normale. L'auteur est aussi porté à croire qu'il existe chez les autres *Eudrilidae*. Chez l'espèce en question les spermatozoïdes migrent de la spermathèque, où ils ont été déposés au cours de l'accouplement, à travers les parois dans l'ovisac, l'entonnoir femelle et l'oviducte. Ce processus est généralement accompagné d'une forte phagocytose.

D'un autre côté, si nous supposons, que chez les Oligochètes, que nous avons étudiés, l'autofécondation est un processus interne, nous serons en face du problème suivant.

On peut croire que la migration des spermatozoïdes des sacs séminaux dans les ovisacs ne s'effectue pas chez les vers qui ont copulé — c'est-à-dire chez les exemplaires, dont les spermathèques renferment du sperme des autres individus. Dans ces cas les propres spermatozoïdes des individus en question doivent être privé d'activité.

Au contraire, si la possibilité de copulation croisée est exclue, nous devons admettre qu'à un certain moment ces spermatozoïdes redeviennent actifs. Nous pouvons nous demander maintenant, de quelle nature est le facteur qui stimule ou déprime cette activité — s'agit-il de l'excitation chimique[1] ou les spermatozoïdes, à un certain stade de leur développement reçoivent-ils la faculté de mouvement indépendemment de l'endroit où ils se trouvent.

Quant aux possibles mécanismes d'autofécondation chez *Eiseniella tetraedra* (s'il est vrai que le développement des œufs sans fécondation croisée ne soit pas dûe à la parthénogénèse mais au processus en question), il est évident que l'autocopulation y fait défaut[2] de sorte que les deux suppositions précitées entrent de nouveau en ligne de compte. D'un côté on peut croire qu'à un certain moment les spermatozoïdes reçoivent la faculté de pénétrer activement à travers les parois des sacs séminaux et à travers les dissépiments, des segments IX, X et XI dans le segment XIII, où se produit la maturation des ovules. D'un autre côté on peut supposer, que l'autofécondation est ici un processus externe qui s'effectue d'une des façons suivantes:

1. Dans le cocon formé autour les segments clitelliens pénètrent les spermatozoïdes (éliminés des pores génitaux mâles, ils suivent les sillons

[1] Il est très probable qu'une action freinante soit exercée sur les spermatozoïdes dans la vésicule séminale par des substances élaborées dans les spermathèques par suite de la résorption des spermatozoïdes d'un autre individu qui y ont été déposés. En connexion avec le problème en question voir les traveaux de L. Černosvitov (1928, 1930 b, 1930 c, 1931).

[2] On pourrait se présenter (à titre d'hypothèse) que l'autocopulation s'effectue chez cette espèce de la manière suivante. Le ver se recourbe à l'endroit entre la région de spermathèques et celle de clitellum en appliquant ainsi les segments, renfermant les spermathèques (X et XI) contre les segments clitelliens (XII—XVII). Le liquide séminal, éliminé des pores génitaux mâles tout en suivant les sillons séminaux atteint la région de clitellum et pénètre ensuite par les sillons intersegmentaires dans les spermathèques, dont les orifices sont situés sur la face dorsale du ver.

séminaux) ainsi que les œufs (par le tube muqueux, entourant le corps du ver).

2. Les œufs seuls (grâce à l'existence du tube muqueux) pénètrent dans le cocon avant qu'il ait quitté les segments clitelliens, tandis que les spermatozoïdes y sont éjaculés au moment où le cocon passe devant les pores génitaux mâles.

Le transport des œufs des pores génitaux femelle dans la région de clitellum pendant la formation du cocon a été décrit chez *Eisenia foetida* (K. Foot et E. Strobell, 1902; A. Grove et L. Cowley, 1926, 1927), où il s'effectue au cours de la reproduction normale. Chez cette espèce les spermatozoïdes n'ont pas été trouvés dans le cocon à l'époque où il entoure encore le clitellum. Ils n'y pénètrent que plus tard, quand le cocon passe devant les orifices des spermathèques (A. Grove, 1927).

Je ne sais pas, si un pareil phénomène existe chez *Eiseniella tetraedra* au cours de la réproduction normale. Autant que j'aie pu me renseigner dans la littérature, il n'est connu jusqu'à présent que chez *Eisenia foetida*. Je considère donc comme peu probables les deux suppositions précitées concernant le mécanisme d'autofécondation chez *Eiseniella tetraedra*.

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3. Les spermatozoïdes pénètrent, suivant les sillons séminaux, dans le cocon, quand il entoure encore le clitellum. Les œufs y sont pondus au moment où le cocon passe devant les pores génitaux femelles.

Cette modalité me paraît aussi peu probable.

4. Les œufs et les spermatozoïdes pénètrent dans le cocon, quand il passe devant les pores femelles (segment XIV) et mâles (segment XIII).

De toutes les modalités, énumérées ci-dessus, cette dernière me paraît être la plus probable.

RÉSUMÉ.

1. Chez les représentants du genre *Limodrilus* l'absence complète ou le développement unilatéral des spermathèques n'ont pas été jusqu'à présent constatés.

2. Chez *Limnodrilus udekemianus* Clap. existe l'autofécondation facultative par autocopulation. Il faut accepter que ce processus s'effectue grâce au repliement du corps entre les segments X et XI et par l'introduction des organes copulatifs dans les orifices des spermathèques. Ce processus est possible grâce à la longueur insignifiante du penis de cette espèce.

3. Chez *Limnodrilus hoffmeisteri* Clap., *L. claparedeianus* Ratzel et *Eiseniella tetraedra f. typica* (Sav.) l'autocopulation n'a pas lieu.

Leurs œufs sont néanmoins capables de passer tous les stades de développement normal sans être fécondés par le sperme d'un autre individu.

On peut expliquer ce phénomène ou par la parthénogénèse ou par l'autofécondation.

Quant à ce dernier processus il peut se présenter ou comme un phénomène interne, s'effectuant grâce à la pénétration des spermatozoïdes des vésicules séminales dans les ovisacs, resp. dans le segment, où murissent les ovules, ou comme un processus externe, dû à l'éjaculation des spermatozoïdes du conduit génital mâle dans le cocon au moment de la ponte.

4. Les individus isolés de *Rhynchelmis limosella* HOFFMSTR. pour qui la fécondation croisée est impossible, éprouvent généralement la régression de l'appareil génital sans éliminer les cocons. Dans des cas très rares les pontes pourtant ont lieu. Les œufs pondus par de pareils exemplaires sont capables de passer les premiers stades de segmentation.

5. Dans les œufs de *Limnodrilus hoffmeisteri* CLAP., non fertilisés par les spermatozoïdes d'un autre individu, les processus de maturation et de développement présentent exactement la même marche que dans les œufs fertilisés par voie de fécondation réciproque. Dans les deux cas les deux globules polaires sont expulsés et la plaque équatoriale de la première et de la deuxième cinèse polaires ainsi que de la première figure de segmentation et des figures suivantes — présente le même nombre de chromosomes bivalents (92).

6. Il faut penser que la réduction du nombre de chromosomes chez *L. hoffmeisteri* s'effectue au moment de l'amphimixie. Le pronucleus mâle s'associe probablement aux caryomères, formés après l'expulsion du second globule polaire et, se fondant avec eux, constitue le noyau de segmentation.

7. Les résultats des recherches cytologiques sur les œufs de *L. hoffmeisteri* exposés ci-dessus ne peuvent pas nous donner la solution du problème qui nous intéresse — sommes-nous chez cette espèce en présence d'autofécondation ou de parthénogénèse.

Or on peut faire sur ce sujet deux hypothèses:

a) Si l'œuf est fécondé, le nombre de ses chromosomes se réduit au moment de l'amphimixie, mais les chromosomes du spermatozoïde le suppléent ensuite.

b) Si l'œuf est resté non fécondé, la réduction du nombre de chromosomes n'a point lieu et le développement s'effectue par voie de parthénogénèse.

8. Les seules preuves décisives en faveur de l'existence de l'autofécondation chez *Limnodrilus hoffmeisteri* et, visiblement, chez les autres Oligochètes, qui ont servi comme matériel pour les expériences en question, seraient la constatation de formation, correspondant aux pronucleus mâle, ou des résidus de spermatozoïdes dans les œufs pondus par les individus isolés, qui n'avaient pas copulé, ou la présence des spermatozoïdes dans les cocons de ces individus. Jusqu'à présent ces constatations n'ont pas réussi.

SUPPLÉMENT.

Au moment, où mon travail était déjà sous presse nous avons constaté avec Monsieur le professeur V. JANDA que la faculté de se reproduire sans fécondation réciproque existe aussi chez *Eisenia foetida*.

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EXPLICATIONS DES PLANCHES.

PLANCHE I.

Fig. 1. Fuseau de la première cinèse polaire avant la ponte. Plaque équatoriale. Apochr. H. I. 90, oc. 4.

Fig. 2. Fuseau de la première cinèse polaire après la ponte. Stade de diaster. Disparition des centrosomes. Imm. $^1/_{12}$", oc. 3.

Fig. 3. Expulsion du premier globule polaire. Commencement de la formation de la protubérance. Centrosomes disparus. Apochr. H. I. 90, oc. 3.

Fig 4. Expulsion du premier globule polaire. Protubérance complètement formée. Apochr. H. I. 90, oc. 4.

Fig. 5. Formation des vacuoles achromatiques autour des chromosomes de l'œuf pendant l'expulsion du premier globule polaire («pseudoreconstruction»). Apochr. H. I. 90, oc. 4.

Fig. 6. Centrosome au pôle interne de la seconde cinèse polaire avec une centriole distincte. Apochr. H. I. 90, oc. 3.

Fig. 7. Fuseau de la seconde cinèse polaire. Plaque équatoriale. Centrosome disparu. Apochr. H. I. 90, oc. 4.

Fig. 8. Deuxième cinèse polaire. Stade de diaster. Apochr. H. I. 90, oc. 4.

Fig. 9. Bipartition anormale du premier globule polaire, dûe à la maturation retardée de l'ovule. Apochr. H. I. 90, oc. 3.

PLANCHE II.

Fig. 10. Expulsion du second globule polaire. Formation de caryomères. Apochr. H. I. 90, oc. 4.

Fig. 11. Expulsion du second globule polaire. Fusion de caryomères. Apochr. H. I. 90, oc. 4.

Fig. 12. Noyau de segmentation. Centrosome vient de se constituer. n — nucleoles, ch — éléments chromatiques. Apochr. H. I. 90, oc. Comp. 6.

Fig. 13. Noyau de segmentation. Constitution de cône polaire (c). Individualisation de chromosomes. Dissolution de la membrane du noyau. Apochr. H. I. 90, oc. Comp. 6.

Fig. 14. Noyau de segmentation. Cône polaire (c) complètement constitué. Chromosomes libres. Apochr. H. I. 90, oc. 3.

Fig. 15. Fuseau de la première figure de segmentation. Plaque équatoriale. Apochr. H. I. 90, oc. 4.

Fig. 16. Représentation parallèle des deux globules polaires expulsés par le même ovule. Le premier globule polaire en haut. Apochr. H. I. 90, oc. 3.

Fig. 17. L'ovule avec les zones (z), dûes aux spermatozoïdes (?). g — premier globule polaire, ch — chromosomes de la seconde cinèse polaire, dispersés dans le résidu du cordon cytoplasmique du fuseau. Obj. 3 (Schroeter), oc. K. 10 ×.

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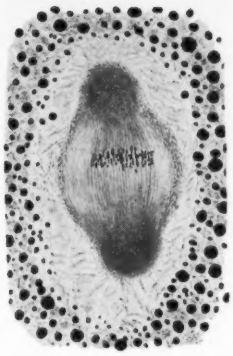

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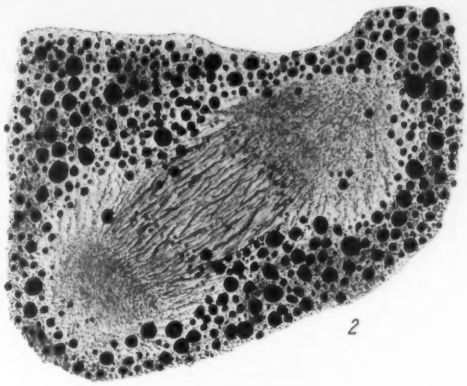

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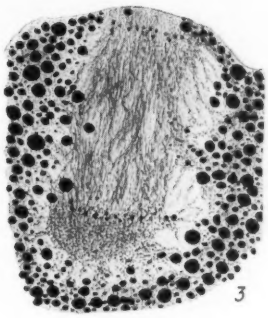

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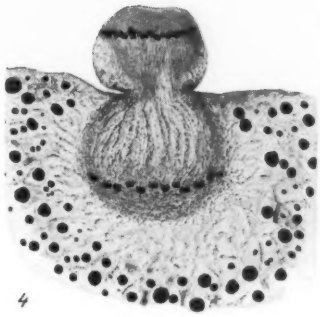

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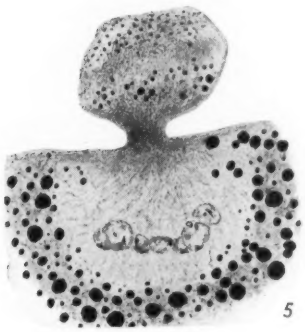

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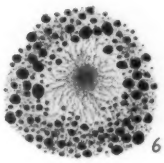

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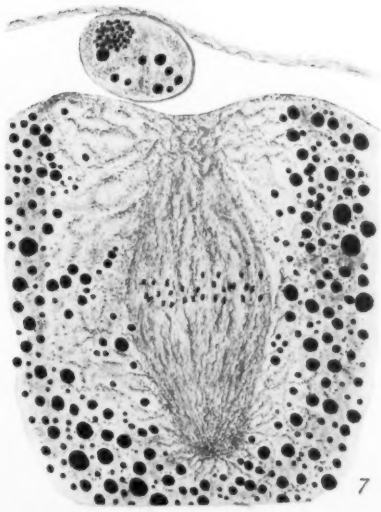

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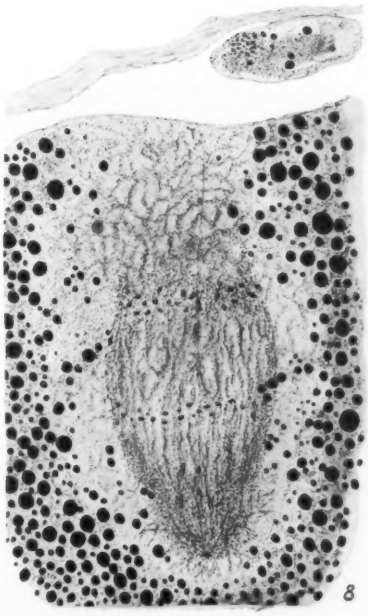

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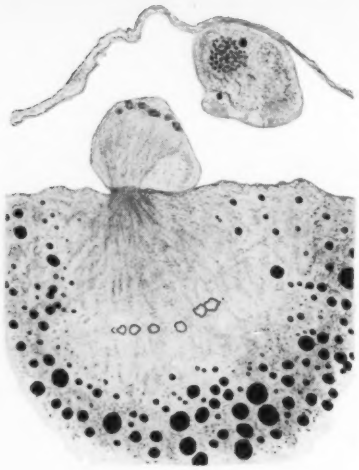

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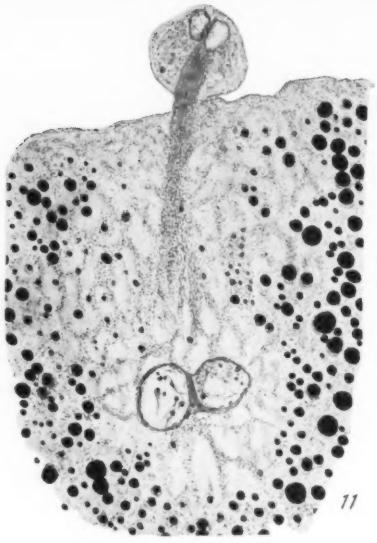

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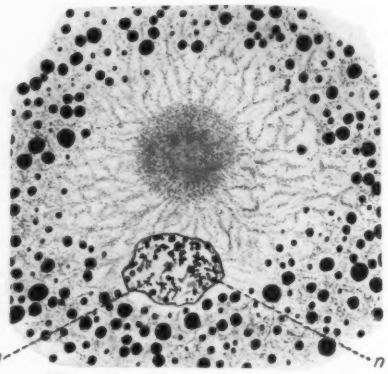

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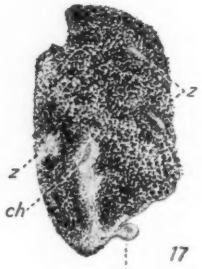

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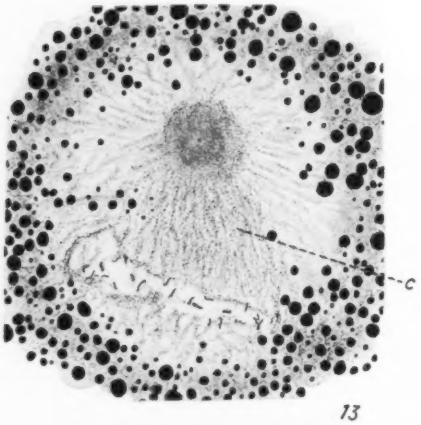

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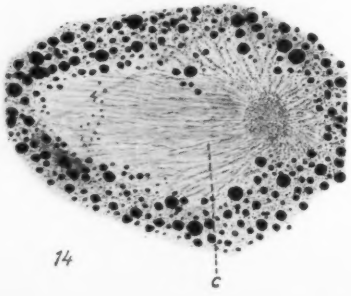

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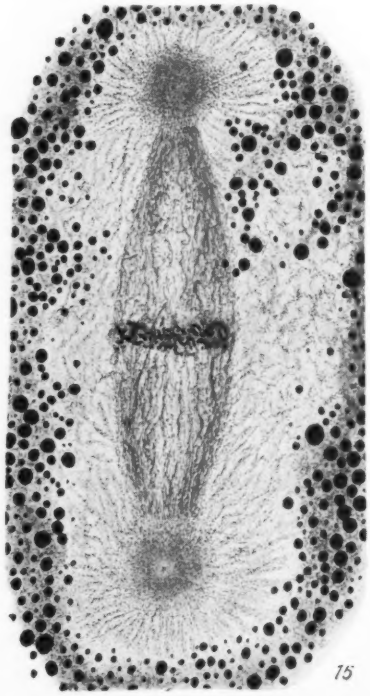

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MORPHOLOGISCHE UNTERSUCHUNGEN DER DECKKNOCHEN DES SCHÄDELS DER WIRBELTIERE

I. MITTEILUNG

SCHÄDEL DER STEGOCEPHALEN

VON

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MIT 36 TEXTABBILDUNGEN

Das umfangreiche Schrifttum über panzerköpfige Amphibien (Stegocephalia) enthält Beschreibungen einer grossen Anzahl des mannigfaltigsten Gattungen dieser Tiere. Die Verfasser der Arbeiten beschreiben gewöhnlich mehr oder minder sorgfältig die Form und das Äussere des Schädels dieses oder jenes Vertreters der Stegocephalia. Jedoch, inwiefern es uns bekannt ist, hat sich keiner von ihnen eigens mit der Erforschung der interessanten Skulptur befasst, die die äussere Oberfläche des Schädels bedeckt. Allerdings beschreiben einige Autoren (FRITSCH, 1879—1885, FRAAS, 1889—1890) mit genügender Ausführlichkeit die Skulptur der Knochen. Immerhin begegnen wir in der Mehrzahl der Fälle im wesentlichen bloss kurzen Hinweisen darauf, die Skulptur an der Schädeloberfläche des in Betracht kommenden Stegocephalen stelle das übliche, die Stegocephalen im allgemeinen kennzeichnende Bild dar. Dahin äussert sich z. B. WATSON (1926) in seiner Beschreibung des unterkarbonischen Stegocephalen *Dolichopareias disjectes*. WIMAN (1914—1917) beschränkt sich in seinen Arbeiten über Stegocephalen der Trias der Insel Spitzbergen auf den Hinweis, die äussere Oberfläche der Schädelknochen wäre bei ihnen mit Grübchen und Furchen bedeckt. Einige Autoren — WATSON (1921), HAUGHTON (1925) — beschränken sich zwecks Veranschaulichung ihrer Arbeiten

auf Abbildungen, die lediglich die Schädelumrisse wiedergeben und interessieren sich keineswegs für die Skulptur der Schädelknochen. I. A. EFREMOV (1932) weist darauf hin, dass die Skulptur der Schädelknochen der Stegocephalen im wesentlichen bislang unerforscht bleibt.

Nicht besser besteht es mit der Erforschung der mikroskopischen Knochenstruktur. In bezug auf diese Frage besitzen wir lediglich sehr fragmentarische Angaben in den Arbeiten von CREDNER (1886—1894).

CREDNERS Befunde sind dermassen mangelhaft, dass das Mikrobild der Belegknochen des Stegocephalen-Schädels bis heute als gänzlich unerforscht gelten darf.

Die sich auf Stegocephalen beziehenden Materialien, welche dem Paläozoologischen Institut der Akademie der Wissenschaften der UdSSR zur Verfügung stehen, ergaben uns die Möglichkeit uns mit dieser Frage zu befassen.

Uns stand zugebote die Sammlung der Originalschädel von *Benthosaurus sushkini Efremov* (sehr gut erhalten), Fragmente von *Trematosaurus brauni Burmeister, Platyops Stuckenbergi Trautschild, Platyops watsoni Efremov, Dwinosaurus Amalitzky* u. a. m.

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Die Gattung *Benthosaurus sushkini* war durch eine beträchtliche Anzahl gesonderter Knochen, Schädelfragmente und, was von besonderem Wert ist, — durch acht vollständig erhaltene vorzüglich abpräparierte Schädel verschiedenen individuellen Alters dargestellt. Ausser den Originalen war im Paläozoologischen Institut eine Reihe von Gipsabgüssen der Stegocephalen-Schädel aus einigen Museum Europas vorhanden.

Die grosse Anzahl der gesonderten Schädelknochen des *Benthosaurus* gewährte die Möglichkeit eine hinreichende Menge von Schliffen zwecks mikroskopischer Erforschung der Knochenstruktur herzustellen.

Ich benutze die Gelegenheit meine volle Anerkennung dem Akad. A. A. BORISSIAK für seine Genehmigung die Materialien des Paläozoologischen Instituts zu verwerten, I. A. EFREMOV für seine freundschaftliche und vielseitige Unterstützung bei dem Studium der Sammlungen und des Schrifttums und J. A. ORLOV für seine wertvollen Ratschläge und seine Kritik zu äussern. Sämtliche Abbildungen sind von dem Verfasser der vorliegenden Arbeit angefertigt.

I.

Die äussere Oberfläche der Belegknochen des Schädels der Stegocephalen ist bekanntlich mit einer charakteristichen rundwabigen Skulptur bedeckt. An einigen Schädelknochen behaupten fast rundliche Grübchen bloss die zentrale Partie der Knochenoberfläche, während sie gegen die Peripherie mehr langgestreckte Umrisse gewinnen und sich hier die Erhabenheiten am

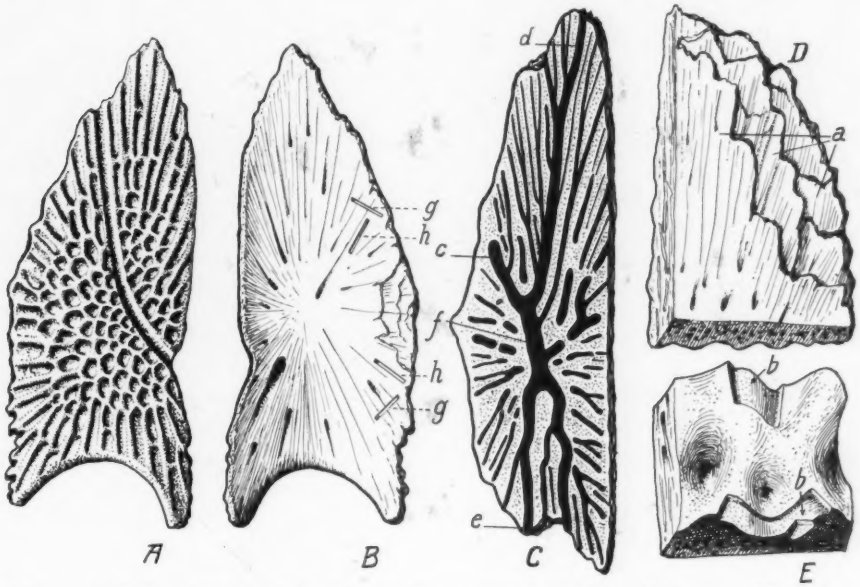

Abb. 1. *A*, *B* Praefrontale sinistrum von Benthosaurus sushkini. (*A* äussere Oberfläche, *B* innere Oberfläche.) *C* System der Kanäle im Frontale dextrum von Benthosaurus. *D*, *E* gesonderte Stücke der Deckknochen von Benthosaurus sushkini. (Vergrössert.)

Knochen als radial gelagerte Kämme gestalten. Ein derartiges Aussehen hat z. B. die Skulptur eines solchen Knochens des *Benthosaurus*, wie das Praefrontale, das auf Abb. 1 (A) dargestellt ist.

Die innere Knochenoberfläche ist von einem ganz andersartigen Bau. Hier gelingt es auf einer fast ebenen Oberfläche lediglich eine sehr schwache radiale Strichelung und ziemlich zahlreiche Öffnungen zu unterscheiden, die als Aus- und Eintrittsstellen der Gefässe dienten.

Die Dimensionen dieser Öffnungen schwanken ungefähr zwischen 1,5 mm im Durchmesser bis auf kaum sichtbare unter der Lupe (Abb. 1 B). In der Richtung nach der Knochenperipherie zu (d. h. gegen die Nähte) geht von einer jeden solchen Öffnung eine lange Rinne ab, deren Breite von dem Durchmesser der betreffenden Öffnung abhängt. Diese sämtlichen Rinnen weichen radial von einem gewissen „Knochenzentrum" auseinander. An der äusseren wabigen Oberfläche entspricht diesem Zentrum eine Region von rundlichen Grübchen. Ist an dem in Betracht kommenden Knochen eine Furche des Schleimkanals vorhanden, so überschneidet sie unbedingt ganz genau dieses Zentrum (Abb. 1 A und B).

Beim Präparieren spalten sich von der Innenseite des Knochens ohne Mühe dünne Lamellen ab, die auf eine schichtige Struktur hinweisen. Derartige Schichten können mehrfach abgetrennt werden, wobei zwischen ihnen sehr feine radial auseinanderweichende Kanäle hervortreten. Auf Abb. 1 B

Abb. 2. Oberfläche des Deckknochens von Benthosaurus sushkini. (Vergrössert um 10mal.)

sind an der rechten Kante der inneren Oberfläche des Praefrontale drei Schichten der abgespaltenen Lamellen dargestellt. Dasselbe Bild, jedoch unter gewisser Vergrösserung, ist auch auf Abb. 1 D wiedergegeben (s. Lamellen a).

In manchen Fällen gelingt es eine derartige Schichtung auch bei der Zerstörung der äusseren wabigen Knochenoberfläche nachzuweisen. Beim Schlage auf den Knochen spalten sich von letzterem mitunter kleine feine Lamellen ab, die genau sämtliche Unebenheiten der äusseren Oberfläche wiederholen (b — Abb. 1 E). Derartige Abspaltungen gelingt es nicht stets zu erzielen, was anscheinend in jedem einzelnen Fall durch gewisse Eigentümlichkeiten der Fossilisation zu erklären ist.

Sind vermöge des Schleifens sämtliche feine Lamellen von der inneren Knochenoberfläche entfernt, so gibt sich in der Tiefe des Knochens, etwa gegen Mitte dessen Dicke das Bild eines ganzen Systems von breiten Kanälen kund, die gewöhnlich mit Gestein angefüllt sind. Auf Abb. 1 C ist das rechte Frontale mit eröffneten Kanälen dargestellt. Der Knochen gehört *Benthosaurus sushkini* an. Der Kanal C (Abb. 1 C) mündet an der inneren Knochenoberfläche, was bereits vor dem Schleifen sichtbar war; die Kanäle d und e verbanden sich offenbar mit einem gleichen System der Kanäle der angrenzenden Knochen, der erste ging in das Nasale, der zweite in das Parietale über. Der breiteste Teil des Kanals (f) ist im Knochenzentrum gelegen, d. h.

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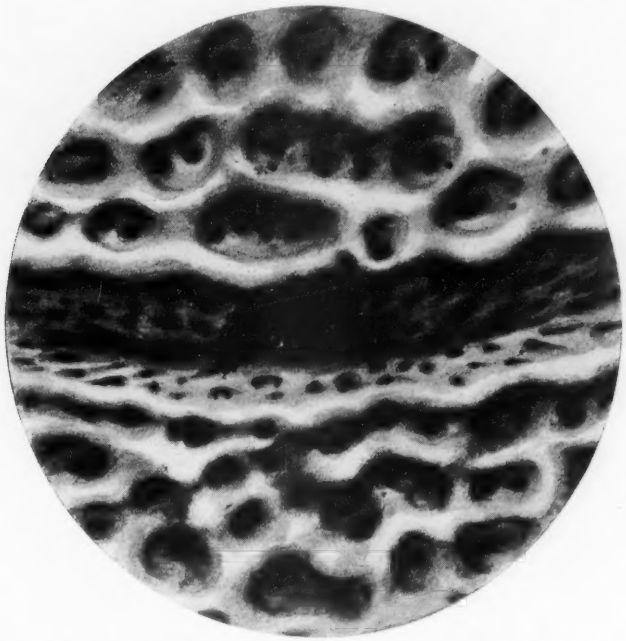

Abb. 3. Oberfläche des Deckknochens von Benthosaurus sushkini. Die Furche des Schleimkanals ist sichtbar. (Vergrössert um 10mal.)

auf derjenigen Stelle, der an der äusseren Oberfläche die Region der runden Waben mit dem sie durchkreuzenden Schleimkanal, an der inneren — der Punkt, aus welchem, wie aus einem Zentrum, die Furchen sich radial erstrecken, entspricht. Die Äste dieses inneren Zentralkanals (f) richten sich gleichfalls radial nach der Knochenperipherie zu. Gewöhnlich sind sie n i c h t in einer Fläche gelagert; eine Gruppe dieser Äste weicht zu der inneren Knochenoberfläche ab, wo sie mit einer Reihe von Öffnungen mündet (Abb. 1 B), die andere — reicht näher an die äussere Oberfläche und findet in Gestalt eines speziellen Kanalsystems ihren Abschluss, das im nachstehenden eingehend besprochen wird.

Bei der Erforschung der wabigen Knochenoberfläche des *Benthosaurus* vermöge einer Lupe (Abb. 2) sind auf dem Boden der einzelnen Waben eine oder mehrere Öffnungen sichtbar, die zum Austritt der Gefässe in die Hautdecke des Schädels dienten. Die die Grübchen abgrenzenden Kämme sind ebenfalls mit Öffnungen besät. Letztere stehen denjenigen auf dem Boden der Waben gelegenen an Umfang um vieles nach, doch sind sie weitaus zahlreicher.

Die auf Abb. 2 dargestellten feinen Öffnungen an den Kämmen lassen sich bloss in denjenigen Fällen nachweisen, wo das dunkler gefärbte Gestein in sämtliche, selbst winzigste Knochenkanäle eindringt.

Auf Abb. 3, die ebenfalls die äussere Knochenoberfläche des *Benthosaurus*, jedoch unter etwas geringerer Vergrösserung wiedergibt, sind diese Öffnungen nicht sichtbar, obschon die ihnen entsprechenden feinen Kanäle, wie es die Untersuchung des Knochenschliffs gezeigt hat, auch hier vorhanden sind.

Die feinen Kanäle der Kämme an den Benthosaurus-Knochen erwiesen sich bei weitem nicht in sämtlichen Fällen mit dunkelgefärbtem Gestein ausgefüllt. Weitaus häufiger beobachteten wir an der Knochenoberfläche ein dem auf Abb. 3 dargestellten analoges Bild und viel seltener gelang es uns einen Knochen zu ermitteln, auf welchem die Austrittsstellen der feinen Kanäle an die Oberfläche gut sichtbar waren (Abb. 2). Dieser Umstand scheint offenbar die Tatsache zu erklären, dass die feinen Öffnungen an der äusseren Oberfläche der Schädelknochen der Stegocephalen bloss einmal von FRITSCH (1885) bei *Dendrerpeton deprivatum* verzeichnet worden sind.

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Längs dem Verlaufe der Furche des Schleimkanals übertrifft die Anzahl der grossen Öffnungen bei weitem diejenige in den anderen Knochenabschnitten (Abb. 3). Werden diese Öffnungen als Austrittsstellen der Gefässe und Nerven betrachtet, so ist es anzunehmen, dass der Schleimkanal des Stegocephalen ungleich reichlicher als die Haut vaskularisiert und innerviert war. Von Interesse ist auch, dass im Bezirke der Furche des Schleimkanals, der oberhalb des Ossifikationszentrums des Knochen gelagert ist, die Öffnungen rundliche Umrisse aufweisen, während sie mit der Entfernung von diesem Zentrum eine mehr ovale Form gewinnen und an jeder Öffnung eine Rinne hervortritt. Auf Abb. 3, wo die Mitte der Furche des Schleimkanals dem Ossifikationszentrum entspricht, ist diese Eigentümlichkeit der Form der Öffnungen gut sichtbar.

Von hohem Interesse sind die Bilder der mikroskopischen Struktur der Schädelknochen des *Benthosaurus*.

Auf Abb. 4 ist der Querschliff eines kleinen Abschnitts des Supratemporale von *Benthosaurus* veranschaulicht. Wie es auf dem Schliff zu ersehen ist, sind die Kämme (a) der Wabenskulptur der äusseren Oberfläche durch eine Reihe von Schichten der Knochensubstanz gebildet. Wie bereits erwähnt können namentlich diese Schichten leicht abgespalten werden (s. Abb. 1 D, Abspaltungen b, b).

Die schichtweise gelagerten Kämme (a) bei *Benthosaurus* sind von einem ziemlich dichten Netze der miteinander anastomosierenden schmalen Kanäle durchzogen (c — Abb. 4). An der Peripherie des Kammes münden diese Kanäle vermöge zahlreicher Öffnungen an der Knochenoberfläche. Erweist sich das System dieser Kanäle mit dunkelgefärbtem Gestein angefüllt, so haben deren Austrittsstellen an die Oberfläche das Aussehen von einer grossen Menge feiner Punkte (Abb. 2).

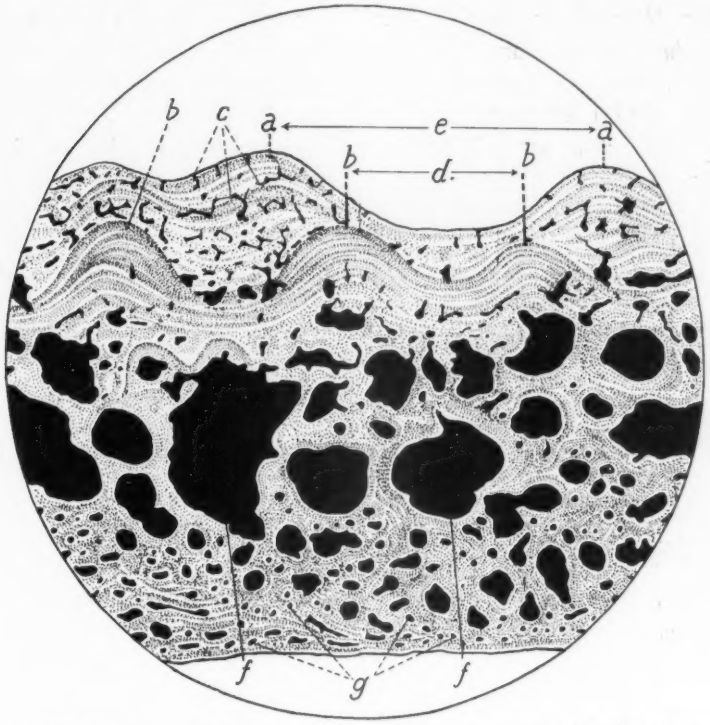

Abb. 4. Querschliff des Supratemporale von Benthosaurus sushkini. (Vergrössert um 30mal.)

In den Schädelknochen der relativ alten Vertreter von *Benthosaurus* gelingt es ausser den Kämmen der äusseren Oberfläche (a) unter ihnen ein System von Kämmen der früheren Generation nachzuweisen (b, b, b — Abb. 4). Sie sind von einer gleichen schichtigen Struktur, wie die Kämme der Oberfläche (a), jedoch von geringeren Dimensionen. Der Abstand zwischen ihren Kuppen (d — Abb. 4) ist stets geringer, als der Durchmesser (e) der von den Kämmen der Oberfläche begrenzten Waben. Somit waren die Waben der früheren Generationen resp. die alten von geringeren Dimensionen, als die späteren. Im Wachstumsvorgange des Knochens erwiesen sich die alten Waben in die Tiefe versunken, da sich oberhalb derselben neue Waben und neue Kämme ausbildeten. Dabei war die Skulptur der früheren Generation nicht resorbiert, sondern blieb in der Knochensubstanz selbst erhalten.

Dieser Prozess erinnert äussert an die Versenkung in den Knochen der Tuberkeln, die den Schädel der Fische aus dem Devon bedecken. Gross (1930) hat das mikroskopische Bild des Knochenbaus von *Coccosteus livonicus* eingehend beschrieben. An den von ihm hergestellten Schliffen sind diese Tuberkeln in der Knochensubstanz als erhalten geblieben zu sehen. Einer

gleichen Versenkung in den Knochen waren auch die Hautzähne von *Dendrodus biporcatus* und *Glyptolepis* unterzogen, bei denen an den Knochenschliffen 4 bis 6 Reihen in der Tiefe des Knochens angelegter Hautzähne zu erkennen sind (Gross, 1930). Der Resorptionsvorgang bei diesen Fischen beeinträchtigt zwar diese Zähne beträchtlich, zerstört sie, jedoch nicht vollständig.

Es ist anzunehmen, dass die Erhaltung der Kämme der früheren Generation in den Knochen der Stegocephalen ein Merkmal der Primitivität der Struktur der Schädelknochen dieser Vertreter der Tetrapoda darstellt, da bei ihnen, gleichwie bei den Fischen aus dem Devon, wenigstens in den äusseren Schichten kein dermassen kompletter Umbau des Knochens beobachtet wurde, der die frühere Skulptur gänzlich zum Schwunde gebracht hätte. Was die tieferen Knochenschichten des *Benthosaurus* anbelangt, so gelingt es hier gewöhnlich nicht Spuren der noch früheren Generationen der Kämme zu entdecken. Sichtbar werden sie bei der Entstehung der grossen Kanäle total zerstört (ff — Abb. 4; c, d, e, f — Abb. 1 C).

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Die breiten Kanäle innerhalb des Knochens (f — Abb. 4) lagern sich etwa gegen dessen Mitte. Hier ist der Knochen am meisten umgebaut. Unter dem Mikroskop sind in der Mitte des Knochens gewöhnlich zahlreiche Reste der Systeme der Knochenlamellen verschiedener Generationen gut sichtbar.

Je näher der inneren Knochenoberfläche, um so geringer werden die Durchmesser der Kanäle. Die feinsten Kanäle (g) liegen gewöhnlich im Bereiche derjenigen dünnen Lamellen, die, wie bereits erwähnt, ohne Mühe sich an der Innenseite des Knochens abspalten lassen.

Wird ein Schliff von einer beliebigen Stelle des Knochens senkrecht zur radialen Strichelung an dessen inneren Oberfläche hergestellt (g, g — Abb. 1 B), so erweisen sich sämtliche Kanäle quer durchschnitten; es kommt dabei ein Bild zustande, das demjenigen auf Abb. 4 analog ist (s. Kanäle f und g).

Derartige Schliffe bezeichnen wir als „Querschliffe", obschon sie sich bei weitem nicht in sämtlichen Fällen quer über der Längsachse des Knochens lagern. Wird dagegen der Schliff längs der radialen Strichelung hergestellt (h, h — Abb. 1 B), so erweisen sich sämtliche Kanäle ihrer Länge nach durchgetrennt. Einen derartigen Schliff werden wir des weiteren der Kürze wegen als „Längsschliff" bezeichnen, obschon er selbstredend nicht stets längs der Längsachse des Knochens gelegen ist.

Das mikroskopische Bild eines derartigen „Längsschliffs" ist auf Abb. 5 wiedergegeben.

Am Schliff sind die Enden zweier angrenzenden Knochen zu ersehen und die zickzackige Spalte (d-d-) bildet die Naht zwischen ihnen. Die grossen und kleinen Knochenkanäle (e — Abb. 5) erstrecken sich längs dem Schliff. Am „Längsschliff" sind von besonderem Interesse die schrägen Kanäle (b),

die an den „Querschnitten" sich nicht verfolgen lassen. Diese Kanäle ziehen in schräger Richtung nach oben und münden am Boden der Senkungen zwischen zwei angrenzenden Kämmen (c). Deren Öffnungen entsprechen denjenigen Austrittsstellen der Knochenkanäle, die auf dem Boden einer jeden Wabe bei Betrachtung des Knochens von der Oberfläche gut sichtbar sind (s. Abb. 2 und 3).

Die in den schrägen Kanälen liegenden Gefässe (b — Abb. 5) spielen offenbar eine grosse Rolle im Vorgange der Ausbildung der Wabenskulptur an der äusseren Knochenoberfläche.

Am Schädel eines sehr jugendlichen *Benthosaurus* (die Gesamtlänge des Schädels beträgt 27,5 mm) hat das Nasale noch keine Wabenskulptur (Abb.

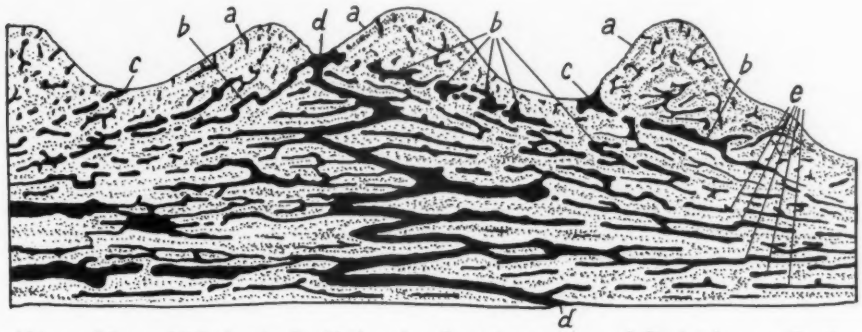

Abb. 5. Längsschliff durch die Enden des Supratemporale und Parietale von Benthosaurus sushkini. (Vergrössert um 20mal.)

6 A). An diesem Knochen ist gut zu ersehen, wie aus dem Ossifikationszentrum radial nicht hohe Kämme auseinanderweichen, die gleichsam das „Haversche System" der vom Zentrum und der Peripherie ziehenden Kanäle darstellen. Jeder von diesen Kanälen mündet an der äusseren Knochenoberfläche mit einer Öffnung, von welcher bis zum Knochenrande eine Rinne verläuft, wo anscheinend die Gefässe und Nerven für die Hautdecke des Kopfes angelegt waren. Diese Kanäle im Knochen der jugendlichen Stegocephalen entsprechen offenbar den „schrägen" Kanälen der erwachsenen (b — Abb. 5).

Des weiteren tritt im Wachstumsvorgange am Knochen eine rundwabige Skulptur auf, die sich über das „Haversche System" der schrägen Kanäle auflagert. Dabei bilden sich die die Waben abgrenzenden Kämme vermöge einer Aufschichtung der Knochensubstanz, in Gestalt einer Reihe Lamellen, die von einem dichten Netz der miteinander anastomosierenden feinen Kanälchen durchbohrt sind, welch letztere aus den „schrägen" Kanälen (b) ihren Anfang nehmen. Als Folge des Auftretens der Kämme am Knochen erweisen sich die Austrittsstellen der „schrägen" Kanäle auf dem Boden der neugebildeten Waben (Abb. 6 B).

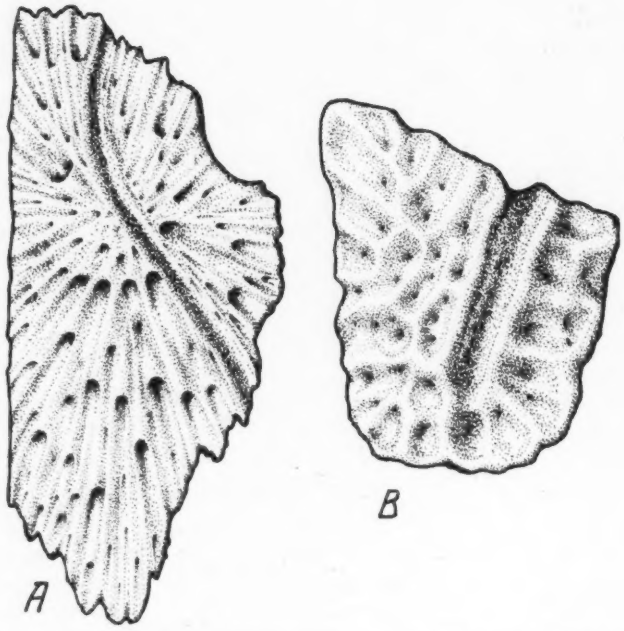

Abb. 6. *A* Nasale dextrum und *B* Supratemporale dextrum eines jungen Benthosaurus sushkini. Gesamtlänge des Schädels = 27,5 mm. (Vergrössert um 10mal.)

Auf Grund der Erforschung einer Reihe von „Quer"- und „Längsschliffen" an verschiedenen Deckknochen des Benthosaurus-Schädels sind wir imstande ein Gesamtschema der Knochenstruktur vorzulegen.

Ein derartiges Schema ist auf Abb. 7 dargestellt:

Der aus gebogenen Knochenlamellen bestehende Kamm „a—a" enthält ein Netz von feinen Kanälchen „b—b". Letztere sind sowohl an den „Quer"- als auch den „Längsschnitten" gleich gut sichtbar. Die Zähigkeit des Gesamtbildes des Kanälchennetzes „b", welch immer die Fläche des Knochenschleifens auch sein mag, zeugt davon, dass dieses Netz nicht entsprechend irgendeiner Achse des Knochens in dessen Totalität orientiert ist. Die Kanälchen „b" münden an der äusseren Knochenoberfläche mit zahlreichen Öffnungen „c", die in einigen Fällen selbst bei geringer Vergrösserung gut sichtbar sind (Abb. 2). Sowohl am „Längs"- als auch am „Querschnitte" sind Spuren von Kämmen der früheren Generation sichtbar (d, d). Am „Längsschnitt" ist ein unter diesen Kämmen angelegter schräger Kanal „e" zu ersehen, der mit einer grossen Öffnung am Boden der Wabe mündet. Tiefer liegt ein ganzes System paralleler, miteinander anastomosierender Kanäle „f". Im Knochen in der Totalität weichen sie radial von dem Ossifikationszentrum auseinander (s. Abb. 1 c). An dem „Querschnitt" können diese Kanäle in zwei Gruppen eingeteilt werden — breite Kanäle „g—g", die ungefähr in der Mitte des

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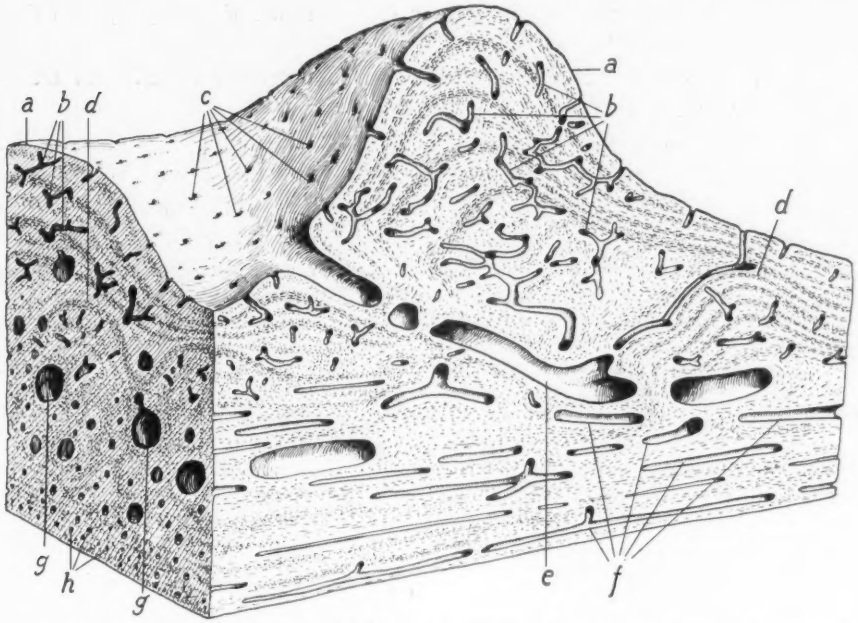

Abb. 7. Schema des Baues des Schädeldeckknochens eines erwachsenen Benthosaurus sushkini.

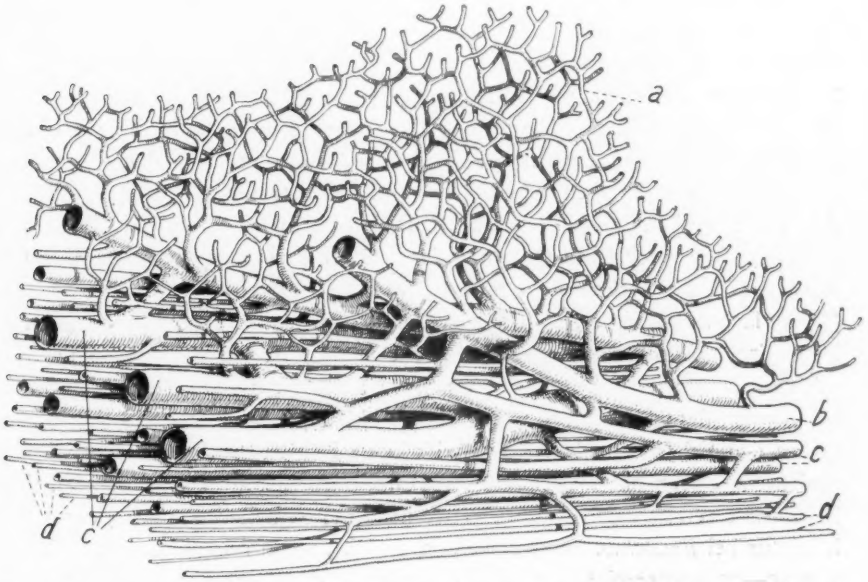

Abb. 8. Schema des Systems der Känale der Deckknochen des Schädels von Benthosaurus sushkini.

Knochens gelagert sind, und eine grosse Anzahl feiner Kanäle „h", die näher zur inneren Oberfläche liegen.

Auf Abb. 8 ist das Schema der Kanäle desselben Anteils des Deckknochens von *Benthosaurus* dargestellt.

Die Knochensubstanz ist auf dem Schema nicht wiedergegeben, es ist lediglich ein System der Kanäle abgebildet. Der Buchstabe „a" bezeichnet hier das Netz der miteinander anastomosierenden Kanälchen des Kamms; „b" — den schrägen Kanal, der mit einer Öffnung am Boden der Wabe mündet; „c" — die Gruppe der breiten Kanäle, die in der Mitte des Knochens verläuft, und „d" — die Gruppe der feinen Längenkanälchen. Zwischen den grossen (c) und den kleinen (d) Kanälen besteht eine Reihe Anastomosen. Letztere sind auch zwischen den Kanälen je einer Gruppe vorhanden.

CREDNER (1894) hatte während der Erforschung von *Sclerocephalus labyrinthicus* die Möglichkeit in den halbzerstörten Bezirken der Schädelknochen einige von den bereits beschriebenen Kanaltypen zu beobachten. Er sah grosse Längenkanäle (c — Abb. 8) und schräge Kanäle (b); er hat die Tatsache verzeichnet, dass die schrägen Kanäle an dem Boden der Waben münden. Ein dichtes Netz der Kanälchen in den Kämmen und feine Kanäle in den Lamellen an der inneren Knochenoberfläche gelang es dagegen CREDNER nicht nachzuweisen, da diese Kanäle von zu geringen Durchmessern sind, um bei Anfüllung mit Gestein in Gestalt des sog. Steinkerns bestehen zu bleiben und ohne Schliffe wahrgenommen zu werden.

An *Branchiosaurus amblistomus* aus dem Oberkarbon, der seinerzeit (1886) von CREDNER eingehend beschrieben worden war, lassen sich zwei Stadien der individuellen Entwicklung gut unterscheiden, und zwar vor der Metamorphose und nach derselben. CREDNER stellt eine Reihe von Unterscheidungsmerkmalen zwischen der noch mit Kiemen atmenden Larve und dem bereits mit Lungen atmenden Tiere fest. Die Branchiosaurus-Larve, deren Länge nicht 60—70 mm übertrifft, hat einen kürzeren und stumpferen Schädel, einen Scleralring ohne Scleralpflaster, eine ovale Form der Orbiten, einen langen Schwanz usw. (Der Schwanz der Larve beträgt ⅔ der Gesamtlänge des Tieres, während er nach der Metamorphose bloss ⅓ gleich ist.) CREDNER rechnet dabei den Merkmalen der Larve das Fehlen der Wabenskulptur nicht zu. Immerhin wäre aus seinen Befunden anscheinend zu folgern, dass die schwache radiale Strichelung, die an der äusseren Oberfläche der Schädelknochen der zweifellosen Larven vorhanden ist, lediglich nach dem Übergange des Tieres zur Lungenatmung durch eine rundwabige Skulptur ersetzt wird. CREDNER weist in seiner Arbeit darauf hin, dass diese Skulptur bei *Branchiosaurus* erst dann auftritt, wenn sein Schädel eine Länge von 20—23 mm erreicht. Jedoch betrachtet er den *Branchiosaurus* mit einem 17 mm langen Schädel als solchen, der bereits das Stadium der Metamor-

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phose durchgemacht hat. Somit kommt die Wabenskulptur erst nach dem Verlust der Kiemen zum Vorschein.

Aus der Durchsicht der Literatur ergab sich die Folgerung, dass in sämtlichen Fällen, wo bei irgendeinem Stegocephalen zweifellose Skelettreste des Kiemenapparats vorhanden sind, die äussere Oberfläche dessen Schädelknochen einer gut ausgeprägten Wabenskulptur ermangelt und umgekehrt, in denjenigen Fällen, wo gänzlich geformte Waben bestehen, die Reste des Stützapparates der Kiemen gewöhnlich nicht nachgewiesen werden. Dies berechtigt uns das Vorhandensein eines Zusammenhangs zwischen dem Charakter der Knochenskulptur und der Metamorphose zu vermuten.

Entspricht diese Voraussetzung der Wirklichkeit, so stellen wir uns den Vorgang der Knochenwachstums folgendermassen vor.

Vor allen Dingen treten am Knorpelschädel des Stegocephalen dünne Lamellen der sich aus dem Bindegewebe entwickelnden Knochen auf. Eine jede derartige Lamelle ist von winzigen Kanälchen durchsetzt, die vom Ossifikationszentrum radial auseinanderweichen und schräg an deren inneren und äusseren Oberfläche münden. Dies gewährt das Bild einer radialen Strichelung sowohl an der äusseren als auch an der inneren Knochenseite. Mit dem Wachstum des Stegocephalen legen sich auf den Knochen an dessen beiden Seiten neue Schichten dünner Lamellen; der Knochen nimmt allmählich an Dicke zu und wuchert zugleich an der Peripherie. Nach der Metamorphose ändert sich scharf der Charakter der Ablagerungen der Knochensubstanz an der äusseren Oberfläche. Der neugebildete Knochen enthält grosse Kanäle. Letztere weichen ebenfalls vom Ossifikationszentrum radial auseinander und münden mit grossen Öffnungen an der äusseren Knochenoberfläche. Ein derartiges Bild sehen wir am Nasale (Abb. 6 A) bei einem sehr jugendlichen *Benthosaurus*, der jedoch bereits mit den Lungen geatmet hat. An dem diese grossen Kanäle enthaltenden Knochen treten späterhin Kämme auf, die unerhebliche Grübchen begrenzen. Auf solche Weise bildet sich die Wabenskulptur aus. Bei dem jugendlichen *Benthosaurus*, dessen Nasale auf Abb. 6 A wiedergegeben ist, weisen die Knochen des postorbitalen Abschnitts bereits diese erste Generation der Wabenskulptur auf (Abb. 6 B). Sie kommt hier früher als im präorbitalen Abschnitt zur Vorschein aus Gründen, die im nachstehenden besprochen werden.

Die Kämme der Wabenskulptur wachsen vermöge Ablagerungen von dünnen Knochenschichten an ihrer Oberfläche und werden mit dem Wachstum von einem dichten Netz schmaler Kanäle durchsetzt. Auf die geformten Kämme der ersten Generation lagert sich in der Folge ein System neuer Kämme, die sich von den ersten durch grössere Dimensionen unterscheiden lassen. Der Abstand zwischen zwei angrenzenden Kämmen nimmt gleichfalls zu, was einen grösseren Durchmesser der Waben der zweiten Generation bedingt. In jeder neuen Generation nehmen die Dimensionen der Kämme

und der Durchmesser der Waben immer mehr zu. Dieser Vorgang geht bei den Stegocephalen offenbar dem Gesamtwachstum des Tieres parallel vor sich, da in Anbetracht der Benthosaurus-Knochen der Wabendurchmesser anhaltend mit der Vergrösserung des Schädels zunimmt. Die Schädellänge von *Benthosaurus* aus den Sammlungen des Paläozoologischen Instituts schwankt zwischen 27,5 mm bis etwa 700 mm. Der Wabendurchmesser beträgt bei dem kleinsten Exemplar 0,2—0,3 mm, bei dem grössten ist er 7,0 mm gleich. Somit bildet sich während des Lebenslaufes des *Benthosaurus* anscheinend eine sehr grosse Anzahl von Generationen der Wabenskulptur und der Wabendurchmesser nimmt unaufhaltsam zu.

Die zwei—drei letzteren Generationen der Kämme bei *Benthosaurus* lassen sich in einigen Fällen bei mikroskopischer Untersuchung der Knochenschliffe nachweisen, während die früheren im Vorgang des Umbaus des Knochens ringsum der in selbigem verlaufenden grossen Gefässe zerstört werden.

Bei dem Stegocephalen verdicken sich die Schädelknochen nicht lediglich auf Kosten des Wachstums nach der äusseren Oberfläche zu. Sie wachsen auch an der Innenseite. Doch bilden sich hier statt der Kämme fortwährend neue dünne Knochenschichten aus, die mit denjenigen der ersten Anlage des Knochens grosse Ähnlichkeiten aufweisen. Sie enthalten schmale, radial vom Ossifikationszentrum auseinanderweichende Kanälchen. Die Schichten der frühen Generationen erreichen die Knochenränder; die sich etwas später ausgebildeten Schichten bedecken dagegen bloss einen gewissen Bezirk in der Region des Ossifikationszentrums. Die Gesamtsumme dieser Schichten bezeichnen wir als „*Basallamelle*".

Von grossem Interesse ist die Tatsache, dass bei relativ jugendlichen Benthosauren an den Vertikalschliffen der Deckknochen des Schädels die Grenze zwischen dieser „Basallamelle" und den darüber gelegenen Knochenanteilen sich unterscheiden lässt.

Ein derartiger Schliff ist auf Abb. 9 wiedergegeben.

Hier stellt die Struktur der Kämme (a) und die Anordnung der grossen Kanäle (b) in der Mitte des Knochens das für den Querschnitt übliche Bild dar. Als Eigentümlichkeit des in Betracht kommenden Präparats tritt die scharfe Abgrenzung (d) der „Basallamelle" (c) gegen den übrigen Knochen auf. Diese Grenze entspricht ihrem Alter nach anscheinend der Metamorphose. Späterhin bei der Ausbildung einer Reihe neuer grosser Kanäle und bei der Veränderung des Durchmessers der alten bringt der Resorptionsprozess diese Grenze total zum Schwunde. An dem auf Abb. 9 dargestellten Schliffe ist ein derartiger Kanal (e), der im Bereiche der „Basallamelle" verläuft, jedoch noch kein eigenes Haversches System besitzt, zu ersehen. In den Knochen der alten Benthosauren hinterlässt diese Grenze bereits keine Spuren (s. Abb. 4) und lediglich die Anwesenheit typischer feiner

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Kanälchen in nächster Nähe zur inneren Knochenoberfläche (g — Abb. 4) zeugt von dem Vorhandensein der Reste der „Basallamelle".

Wie bereits erwähnt, beschränken sich die Verfasser bei Besprechung der äusseren Oberfläche der Deckknochen der Stegocephalen gewöhnlich auf den Hinweis, dass diese Oberfläche mit der sog. Wabenskulptur bedeckt ist.

Lediglich FRAAS verzeichnet bei der Beschreibung der Schädel von *Mastodonsaurus giganteus* (1889—1890) und *Plagiosaurus granulosus* (1913) die Tatsache, dass diese Skulptur in einigen Fällen entsprechend der Richtung des Wachstums des Knochens orientiert ist.

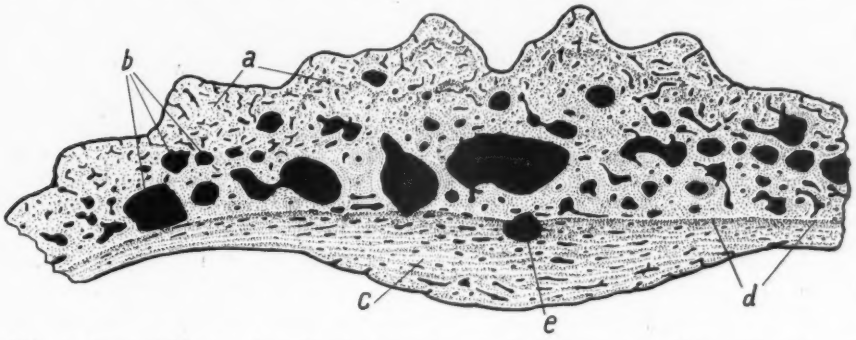

Abb. 9. Querschliff aus dem Quadratojugale von Benthosaurus sushkini. (Vergrössert um 20mal.)

Auf diese kurze Andeutung beschränken sich zur Zeit sämtliche Literaturangaben in bezug auf die gegenseitige Abhängigkeit des Knochenwachstums und der Differenzierung der Skulptur.

Beim Studium der Schädel verschiedener Labyrinthodonten haben wir die Schlussfolgerung gezogen, dass nicht sämtliche ihre Knochen auf gleiche Weise wachsen. Einige derselben nehmen im Wachstumsvorgange gleichmässig nach allen Seiten zu, andere dagegen wachsen in die Länge weitaus mehr als in die Breite. Sowohl in dem einen, als in dem anderen Fall spielt sich bei der Differenzierung der Skulptur eine Reihe sehr interessanter Prozesse ab.

Ein gutes Beispiel des fast gleichmässig intensiv nach allen Seiten wachsenden Knochens stellt das Dermosupraoccipitale dar. Auf Abb. 10 K ist das Dermosupraoccipitale dextrum eines relativ kleinen *Benthosaurus* wiedergegeben. Dieser Knochen ist gleichmässig mit runden Waben bedeckt. Das Dermosupraoccipitale (Abb. 10 L) derselben Stegocephalen-Spezies, jedoch eines älteren Exemplars, ist von grösseren Dimensionen und die es bedeckenden Waben haben einen grösseren Durchmesser im Vergleich zu den Waben des obigen Knochens. Wird das Dermosupraoccipitale aus einem Schädelfragment des grössten der uns bekannten Benthosauren entnommen (Abb. 10 M), so stellt sich heraus, dass bei den grösseren Dimensionen des Knochens

auch der Durchmesser der Waben noch mehr zunimmt. Diese Beobachtungen berechtigen uns folgende zwei Schlussfolgerungen zu ziehen.

Einmal. In den Fällen, wo der Schädelknochen des Labyrinthodonten gleichmässig intensiv nach allen Seiten wächst, wird dessen äussere Gesamtoberfläche gleichmässig mit rundwabiger Skulptur bedeckt.

Sodann. Mit dem Wachstum des Knochens ändert sich die ihn bedeckende Skulptur, was sich in einer Zunahme des Durchmessers der Waben kundgibt.

Dies stimmt volkommen mit dem bereits geschilderten mikroskopischen Bilde der Knochenstruktur überein. Bei der Erforschung der Knochenschliffe war es zu ersehen, dass die späteren Generationen gegen die früheren durch einen grösseren Durchmesser abstechen.

Ein ganz anderes Aussehen hat die Skulptur in den Fällen, wo der Knochen nicht gleichmässig intensiv nach allen Seiten im Wachstum begriffen ist und eine langgestreckte Form erwirbt.

Auf Abb. 10 sind drei Knochen-Dermosupraoccipitale (E), Parietale (F) und Frontale (G) dargestellt, die einem erwachsenen *Benthosaurus* angehören. Dem Charakter der Skulptur nach weichen die zwei ersten dieser Knochen wenig voneinander ab. Die Skulptur des Frontale dagegen weist einige interessanten Besonderheiten auf. An dessen Oberfläche lassen sich dem Charakter des Reliefs nach zwei verschiedene Bezirke unterscheiden. Der eine ist mit der üblichen Wabenskulptur bedeckt, im anderen sind die Waben dermassen ausgedehnt, dass sie sich in lange Rinnen umgewandelt haben, die durch schwach divergierende Kämme abgegrenzt sind.

Die gleichnamigen Knochen eines anderen Labyrinthodonten, *Trematosaurus Brauni* (Abb. 10 B, C und D) weichen gewissermassen von den entsprechenden Knochen des *Benthosaurus* ab. Das Dermosupraoccipitale (B) steht der Form und Skulptur gemäss dem gleichen Knochen des *Benthosaurus* sehr nahe. Das Parietale (c) hat einen stark nach vorne gestreckten Bezirk, der mit langgezogenen Waben und radial divergierenden Kämmen bedeckt ist. Am Frontale (D) sind solcher Bezirke *zwei* — der eine ist nach vorne, der andere nach hinten gerichtet, während die Mitte des Knochens von einer Region runder Waben besetzt ist.

In sämtlichen Fällen, wo irgendein Deckknochen des Labyrinthodonten-Schädels eine längliche Form erwirbt, kommt an dem Knochen ein Bezirk langgestreckter Waben und langer Kämme zum Vorschein. Doch ist die Verlängerung des Knochens zweifellos durch dessen mehr intensives Wachstum in bestimmter Richtung bedingt. Folglich wird auch das Auftreten der Kämme und der langgezogenen Waben durch dieselbe Ursache erzeugt. Somit ist das Vorhandensein der charakteristischen Skulptur ein direkter Hinweis auf das mehr intensive Wachstum des betreffenden Knochenbezirks. Derartige Bezirke bezeichnen wir als „Zonen des intensiven Wachstums".

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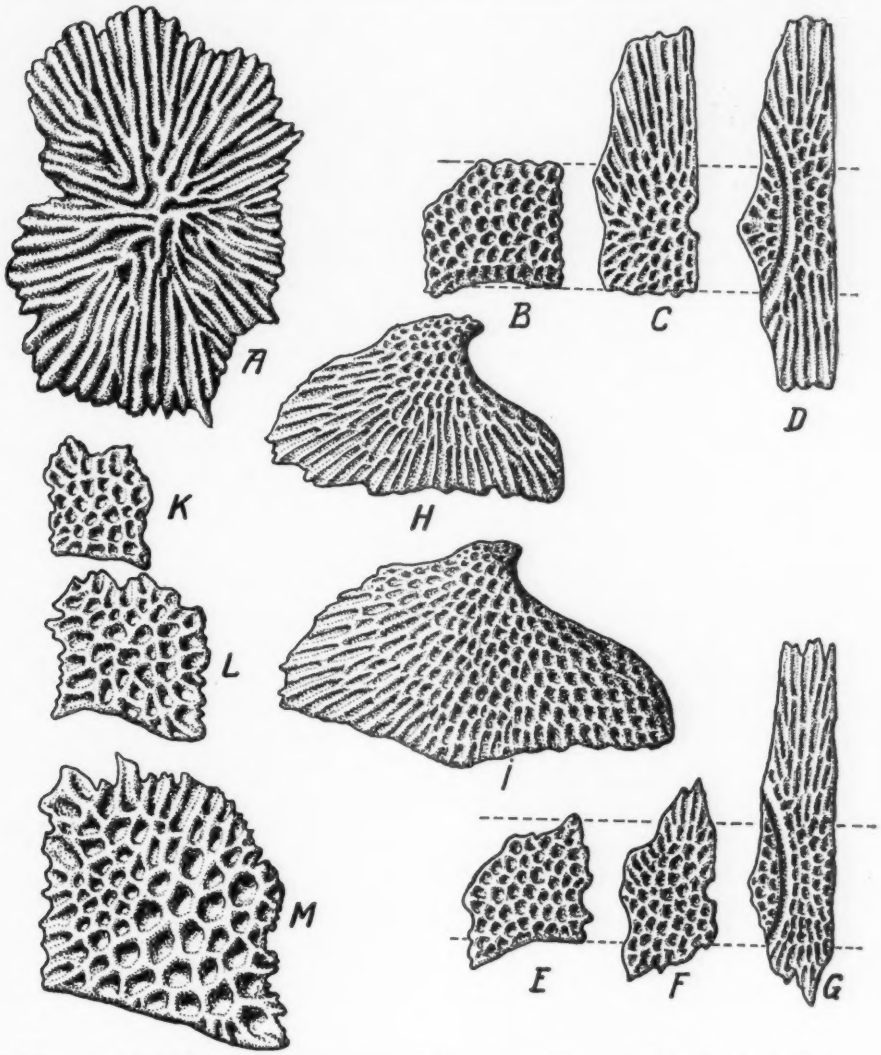

Abb. 10. *A* Parietale dextrum von Dwinosaurus (Nr. 2353-64); *B, C, D* Dermosupraoccipitale, Parietale und Frontale von Trematosaurus Brauni; *E, F, G* Dermosupraoccipitale, Parietale und Frontale von Benthosaurus sushkini; *K, L, M* Dermosupraoccipitalia dextra von Benthosaurus verschiedenen individuellen Alters; *H, J* Squamosa von Benthosaurus sushkini. (Natürliche Grösse.)

An jedem Deckknochen des Labyrinthodonten-Schädels ist obligat ein Bezirk der rundwabigen Skulptur vorhanden. Die Mitte dieses Bezirks ist stets dem Ossifikationszentrum genau konform, dass an der inneren Knochenoberfläche gut sichtbar ist. Infolgedessen bezeichnen wir die Region der runden Waben als „Zentralzone".

Wächst der Knochen an der Peripherie mit gleichmässiger Intensität nach allen Seiten hin, so stellt er seinem Wesen nach lediglich die „Zentralzone" dar und ist durchweg mit runden Waben bedeckt. Desgleichen sind z. B. die Dermosupraoccipitalia von *Benthosaurus* (Abb. 10 E) und *Trematosaurus* (Abb. 10 B). Wir haben bereits gesehen, dass welche Dimensionen dieser Knochen auch immer erreichen mag, seine Oberfläche mit runden Waben bedeckt bleibt.

An den Schädeln der Benthosauren von 142 mm Länge sind die radialen Kämme an Knochen, die Zonen des intensiven Wachstums besitzen, besonders gut ausgeprägt. Bei den älteren (Länge von 210 bis 229 mm und darüber) tritt das für die Zone des intensiven Wachstums übliche Bild nicht so deutlich hervor. Dies findet darin seine Erklärung, dass in der Folge zwischen zwei angrenzenden Kämmen Scheidewände zustande kommen, die die lange Rinne zwischen ihnen in eine Reihe Kammern zerteilen. Als Ergebnis dieses Prozesses bilden sich der Rinne entlang runde Waben aus, die sämtliche charakteristischen Eigentümlichkeiten der Zone des intensiven Wachstums ausgleichen. Als gutes Beispiel dieser Erscheinung bringen wir die Darstellungen des Squamosum zweier Benthosauren verschiedenen Alters (Abb. 10, H und I).

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Am Squamosum des jugendlichen *Benthosaurus* (H) sind die langen Kämme und die dazwischen liegenden Rinnen gut sichtbar. Bei den älteren Vertretern derselben Gattung (I) hat sich bereits eine typische Wabenskulptur ausgebildet und zwar dort, wo bei dem jugendlichen sich die Zone des intensiven Wachstums mit der ihr eigenen kammförmigen Skulptur befand und lediglich im vorderen Abschnitt des Squamosum sind die Kämme erhalten geblieben. Folglich nimmt im Vorgange des Knochenwachstums nicht bloss die Zone des intensiven Wachstums, sondern auch das Areal der rundwabigen Region zu.

Sämtliche Veränderungen der Skulptur im Wachstumsvorgange des Knochens sind in gewissermassen schematisierter Form, inwiefern sie sich auf Grund des soeben besprochenen darbieten, auf Abb. 11 wiedergegeben.

Am Schädeldeckknochen (a), der noch keine Wabenskulptur besitzt, tritt während der postmetamorphosen Periode erstmalig die rundwabige Skulptur auf. Wächst dieser Knochen späterhin gleichmässig intensiv nach allen Seiten (b), so bedecken neue Generationen der runden Waben dessen äussere Gesamtoberfläche und lediglich der Durchmesser der Waben nimmt immer mehr und mehr zu (c). Die fortgesetzte Zunahme des Knochens wird das Gesamtgepräge der Skulptur nicht modifizieren, jedoch die Zunahme des Durchmessers der Waben der neuen Generation hervorrufen (d). Auf solche Weise ändert sich die Skulptur im Falle des gleichmässigen Wachstums des Knochens.

Am Deckknochen, der eine Zone des intensiven Wachstums besitzt, vollziehen sich die Veränderungen an der Skulptur auf eine etwas mehr komplizierte Weise.

Nehmen wir an, dass im Wachstumsvorgange bei der Zunahme des Knochens während eines bestimmten Zeitabschnitts in den neuausgebildeten Bezirken an der Peripherie eine Reihe neuer Waben auftreten soll. Setzen wir ausserdem voraus, dass während derselben Spanne Zeit der Knochenrand um 2 mm wächst, was etwa dem Durchmesser der Waben der in Betracht kommenden Generation entsprechen wird.

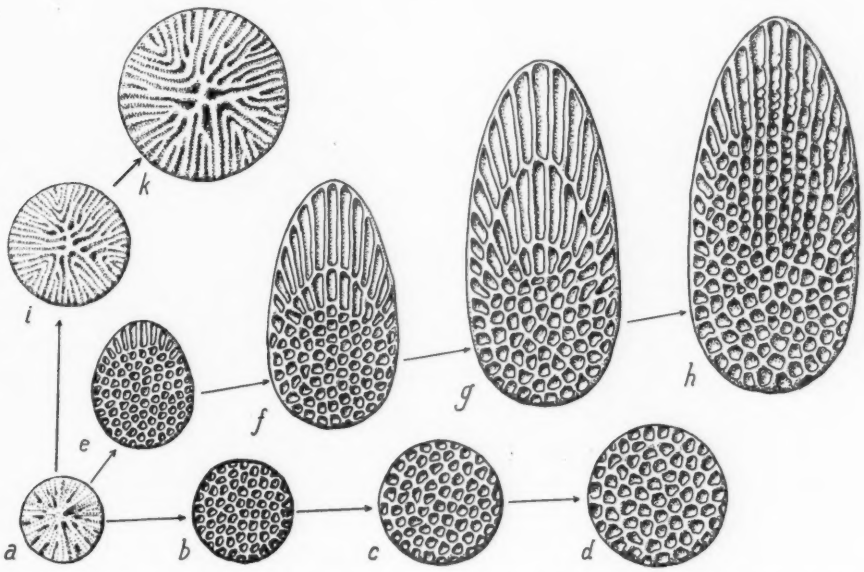

Abb. 11. Schema der Differenzierung der Skulptur des Deckknochens des Stegocephalen-Schädels.

Wuchert der Knochen gleichmässig um 2 mm auf seinem Gesamtperimeter, so tritt an dessen Rändern eine Reihe runder Waben auf. Dauert aber dieser Vorgang fort, so wird es sich gegebenenfalls um das sog. gleichmässige Wachstum des Knochens handeln (b-c-d — Abb. 11).

Nimmt während derselben Wachstumsperiode einer von den Knochenrändern nicht um 2, sondern um 6 mm zu, so bilden sich an dessen Oberfläche nicht 3, sondern bloss eine Reihe Waben aus, welche sich späterhin in lange Rinnen umwandeln (e). Somit ruft die Beschleunigung des Knochenwachstums keine Ausbildung einer grösseren Anzahl der Waben hervor. Das Auftreten der Rinnen (oder der langgestreckten Waben) im Bereiche der Zone des intensiven Wachstums wäre hier durch die Störung der gegenseitigen Beziehung zwischen den Zeitmassen des Knochenwachstums und

denjenigen der Differenzierung der Skulptur an der äusseren Knochenoberfläche zu erklären. Die Beschleunigung der Zeitmasse des Wachstums hat keine Beschleunigung der Differenzierung zur Folge. Welche Grösse der rapide wachsende Knochenbezirk auch erreichen mag, es bildet sich an ihm während ein und desselben Zeitraums nicht mehr Waben aus, als an einem langsam wachsenden Bezirke. Dabei beeinflusst die Beschleunigung des Wachstums lediglich die Form der Waben, sie in lange Rinnen umwandelnd. Je intensiver das Wachstum des Knochenrands, um so länger werden die ihn bedeckenden Waben.

Zugleich mit diesem Vorgang geht auch eine Ausbildung neuer Generationen der Waben von statten. Dies erschwert den Gesamtprozess der Differenzierung der Skulptur in erheblichem Grade. In jedem neuen Stadium (f, g) handelt es sich im wesentlichen um eine neu ausgebildete Struktur, die nichtsdestoweniger das frühere Gesamtgepräge des Reliefs beibehält und sich bloss durch einen grösseren Durchmesser der runden Waben und eine grössere Breite der Rinnen unterscheiden lässt.

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Bei den alten Labyrinthodonten gesellt sich diesen sämtlichen Vorgängen noch das Phänomen der supplementären Differenzierung der Skulptur hinzu. Dabei tritt auf dem Boden der langen Rinnen, angefangen von der zentralen Knochenzone, eine Reihe Querscheidewände auf. Als Ergebnis bilden sich den Rinnen entlang runde Waben aus (h). Solches zeugt offenbar von einer Verlangsamung der Zeitmasse des Knochenwachstums. Übertrafen bei der Ausbildung der Rinnen die Zeitmasse des Wachstums diejenigen der Differenzierung der Skulptur, so gestalten sich diese Verhältnisse bei der Entstehung der supplementären Differenzierung als umgekehrt, auf Kosten der Verlangsamung der Zeitmasse des Wachstums bei den früheren Zeitmassen der Differenzierung.

Auf solche Weise formt und modifiziert sich die Skulptur an der Schädeloberfläche des *Benthosaurus* und offenbar der Stegocephalen im allgemeinen. Wir hatten jedoch die Möglichkeit eine äusserst interessante Ausnahme aus diesem Gesamtschema der Differenzierung der Skulptur zu erforschen. Es handelt sich gegebenenfalls um den *Dwinosaurus Amalitzky*. Wir werden uns mit den Eigentümlichkeiten dieses Labyrinthodonten im nachstehenden eingehend befassen. Augenblicklich halten wir es für nötig bloss darauf hinzuweisen, dass diese Gattung die Kiemenatmung offenbar lebenslang beibehält und im Grunde genommen eine Larve darstellend, eine vollkommen arteigene Skulptur an der Oberfläche der Schädelknochen aufweist. Diese Skulptur hat das Aussehen radial auseinanderweichender Kämme und stellt sichtbar lediglich eine äusserst gesteigerte radiale Skulptur, die sämtlichen Larven eigen ist, dar (Abb. 10 A, 1 f-k). An den Schädelknochen von *Dwinosaurus*

gelingt es keine einzige runde Wabe nachzuweisen. In Anbetracht des uns zu Gebote stehenden Materials geht die Entwicklung der Skulptur an der Oberfläche der Schädelknochen des *Dwinosaurus* auf einer ganz besonderen Bahn vor sich (a, i, k — Abb. 11).

II.

Die Zonen des intensiven Wachstums der einzelnen Deckknochen des Schädels der Stegocephalen sind nicht ungeregelt an der Schädeloberfläche zerstreckt. Gewöhnlich ordnen sie sich auf solche Weise, dass aus den Wachstumszonen der einzelnen Schädelknochen in der Totalität sich eine Gesamtzone des Wachstums zusammensetzt. Mit anderen Worten — bilden die Zonen des intensiven Knochenwachstums eine Zone (bzw. Zonen) des intensiven Wachstums des Schädels als Ganzes.

Zwecks Klärung der Bedeutung der Zone des intensiven Wachstums im Vorgange der Schädelausbildung wollen wir uns mit dem Schädel von *Benthosaurus sushkini* befassen, der erstmalig von J. A. Efremov (1929) beschrieben worden ist.

Bei *Benthosaurus* (Abb. 12) bilden die radial gelagerten Kämme an den vorderen Enden der Jugalia, Praefrontalia und Frontalia und an den hinteren Enden der Lacrimalia und Nasalia eine breite Zone des intensiven Wachstums, die zwischen den Augengruben und Nasenlöchern liegt. Zwischen den Orbiten und dem Occipitalrande des Schädels (abgesehen von Squamosa und Quadratojugalia) sind sämtliche Knochen mit einer deutlich ausgeprägten rundwabigen Skulptur bedeckt; keiner von ihnen weist hier eine zur Genüge gut ausgesprochene Zone des intensiven Wachstums auf.

Eine derartige Anordnung der Zone des intensiven Wachstums am Schädel bewirkte bei *Benthosaurus* eine beträchtliche Verschiebung der Schnauzenspitze mitsamt den Nasenlöchern nach vorne.

Burmeister (1850), die Reste von *Archegosaurus Decheni* erforschend, hat als Erster die Tatsache berücksichtigt, dass der Schädel dieses Labyrinthodonten sich im Vorgange des individuellen Wachstums beträchtlich verlängert. Er erbrachte den Nachweis, das Verhältnis der Länge zur Breite wäre bei jugendlichen Exemplaren von 6 zu 5, bei alten von 13 zu 7.

Späterhin hat v. Meyer (1856—1858) auf Grund des Studiums des *Archegosaurus* an einem grösseren Material dieselben Schlussfolgerungen gezogen.

Credner (1886), der zahlreiche Reste von *Branchiosaurus amblistomus* eingehend beschrieben hat, stellte an Hand einer Reihe von Messungen fest,

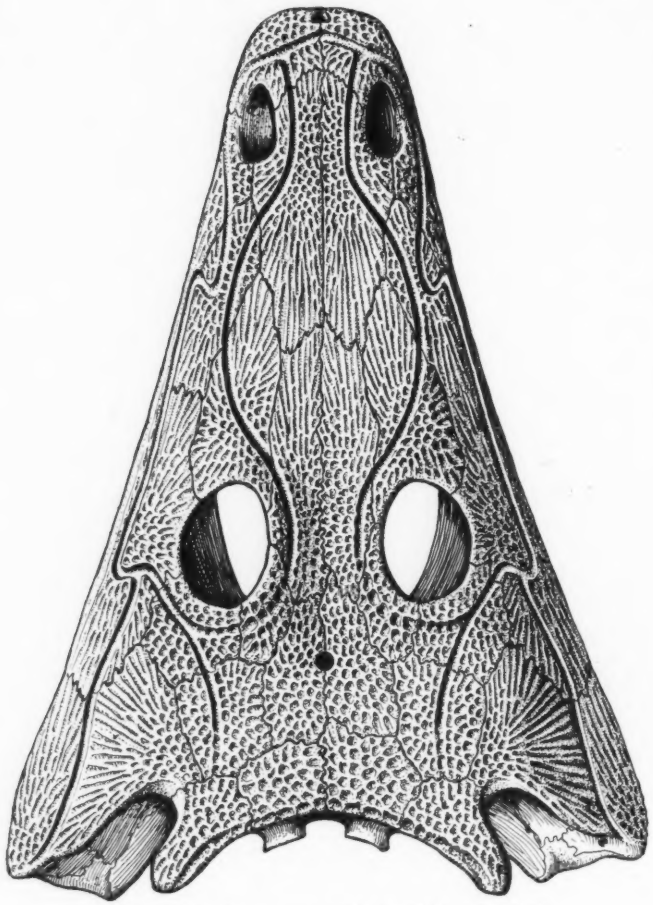

Abb. 12. Benthosaurus sushkini (Nr. 1-9-2283).

dass der Schädel dieser Stegocephalen-Spezies im Wachstumsvorgange eine vierfache Länge erreicht, während die Breite des Schädels im Laufe desselben Zeitraums ums dreifache zunimmt.

Bei der Erforschung der Schädel von *Benthosaurus* war für uns nicht dermassen die Gesamtzunahme des Schädels mit der Altersveränderung, als die Frage nach der Rolle in diesem Vorgang der Zone des intensiven Wachstums von Belang.

Die Messungen dieser Schädel haben erwiesen, dass der präorbitale Schädelteil ungleich rapider, als der postorbitale wächst. Auf Abb. 13 sind zwei Schädel dargestellt; der eine von ihnen hat eine Länge von 140 mm (N 1-9-2283), der andere von 229 mm (N 32-1-2354). Der Hinterhauptsrand der beiden Schädel ist auf einer Horizontale angelegt, die Enden der Schnauze

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sind vermöge einer geraden Linie verbunden. Zwischen der Horizontale und dieser Linie sind fünf gerade Linien gezogen, die die Längen der fünf Benthosaurus-Schädel von 163, 195, 210, 218 und 221 mm darstellen. Auf derselben Abbildung ist die Grenze zwischen den prä- und postorbitalen Regionen des Schädels durch eine punktierte Linie angedeutet. Als Grenze ist die die Orbitalzentren verbindende Linie angenommen. Die Zahlen längs der punktierten Linie bezeichnen die Abstände von selbiger bis zum Hinterhauptsrand des Schädels in Millimetern aus diesem Diagramm erhellt mit

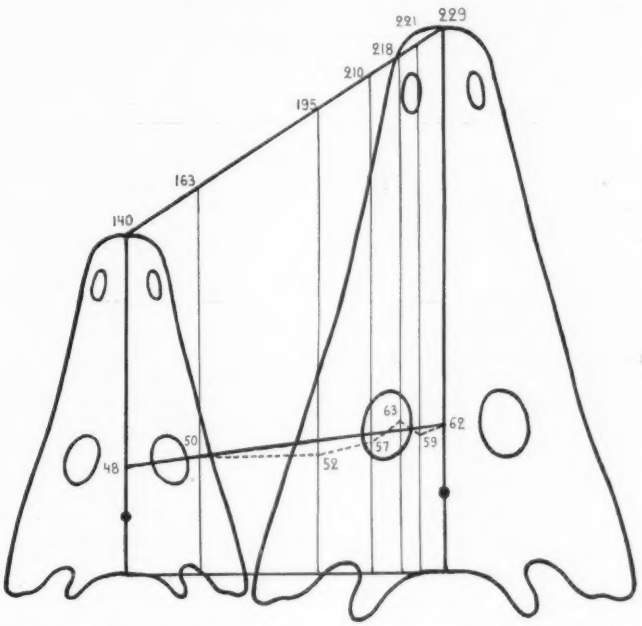

Abb. 13. Schema des Schädelwachstums von Benthosaurus sushkini.

völliger Evidenz, dass das präorbitale Gebiet des Benthosaurus-Schädels im Vorgange des individuellen Wachstums weitaus mehr als das postorbitale zunimmt, was mit der Anordnung der Zone des intensiven Wachstums vollständig konform ist. Letztere ist bei *Benthosaurus* zwischen den Augengruben und den Nasenlöchern gelegen. —

Noch interessantere Zahlen ergaben die Messungen jedes gesonderten Knochens. Zur Vergleichung haben wir drei Schädel des *Benthosaurus* von verschiedenem Alter genommen. Nach der Messung der Länge und Breite des Knochens wurde dessen Index berechnet, wobei als 100 in sämtlichen Fällen die Breite des Knochens galt, die stets der Längsachse des Schädels senkrecht war. Im nachstehenden sind drei Reihen von Zahlen angegeben, die von uns als Ergebnis dieser Berechnungen erzielt worden sind.

Bezeichnung des Schädelknochens	Benthosaurus 140 mm Nr. 1-9-2283	Benthosaurus 163 mm Nr. 7-11-2283	Benthosaurus 210 mm Nr. 32-3-2354	Anmerkung
Nasale	360	400	487	Zone des intensiven Wachstums
Frontale	466	500	620	
Lacrimale	318	372	438	
Praefrontale	261	280	317	
Praemaxillare	116	135	154	Wachstum in die Länge
Maxillare	1100	1120	1138	
Parietale	250	272	284	
Quadratojugale	247	250	260	
Postfrontale	246	245	246	Gleichmässiges Wachstum
Supratemporale	150	150	150	
Dermosupraoccipitale	93	94	94	
Postorbitale	84	85	84	
Tabulare	164	166	167	
Jugale	388	368	353	Wachstum in die Breite
Squamosum	172	155	148	

Aus diesen Indexen ist zu ersehen, dass die durch die Zone des intensiven Wachstums behafteten Schädelknochen von *Benthosaurus* kräftig in die Länge wachsen. Derartige Knochen sind bei *Benthosaurus* das Nasale, Frontale, Lacrimale und Praefrontale. Namentlich an diesen Knochen sind die Bezirke der Zonen des intensiven Wachstums, wo die Wabenskulptur durch die der Längsachse des Schädels entlang ziehenden Kämme ersetzt ist, gut sichtbar (Abb. 12). Ein belangloses Wachstum in die Länge wird auch an solchen Knochen, wie das Praemaxillare und Parietale verzeichnet. Bei aufmerksamer Erforschung der Skulptur an ihrer Oberfläche gelingt es unschwer Bezirke mit radialen Kämmen, d. h. Zonen des intensiven Wachstums, zu ermitteln.

Was das Maxillare und Quadratojugale anbetrifft, so besitzen diese Knochen gewisse Eigentümlichkeiten. Das Maxillare, das mit seinem Ende dem Vorderrande des Quadratojugale anliegt (Abb. 14), wächst dem Gesamtwachstum des Schädels proportional; das mit der Gelenkgegend und den Kaumuskeln verbundene Quadratojugale wächst bei *Benthosaurus* mit dem Alter nicht lediglich nach vorne, sondern nimmt auch ventralwärts zu, was, trotz dem Vorhandensein einer gut ausgeprägten Zone des intensiven Wachstums, ein relativ geringes Vorherrschen des Wachstums in die Länge über demjenigen in die Breite bedingt.

Derartige Knochen der postorbitalen Schädelpartie wie das Postfrontale,

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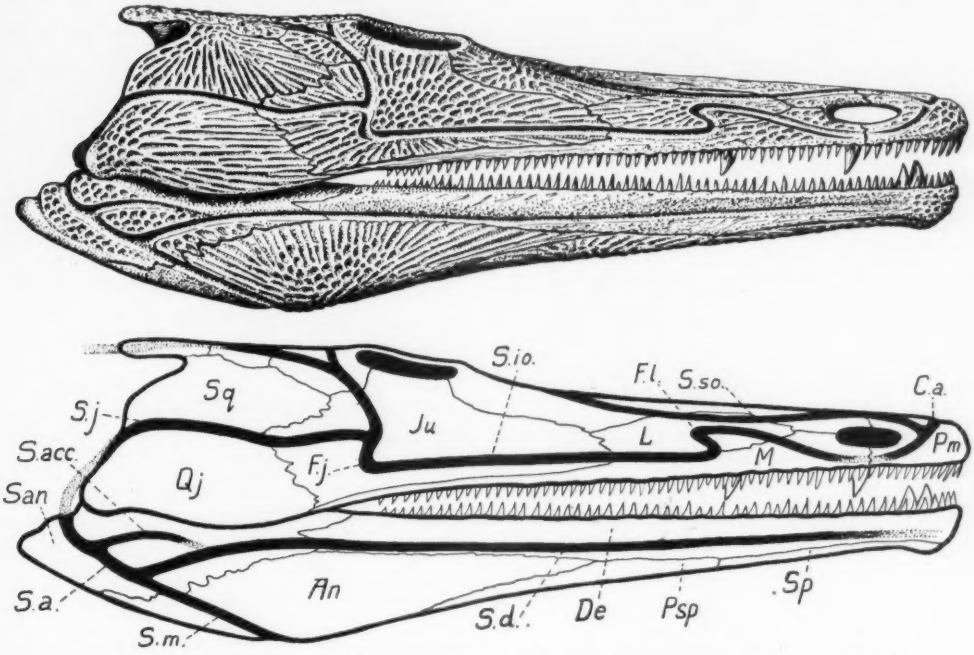

Abb. 14. Benthosaurus sushkini. *Pm.* Praemaxillare, *M.* Maxillare, *L.* Lacrimale, *Ju.* Jugale, *Sq.* Squamosum, *Qj.* Quadratojugale, *San.* Supraangulare, *An.* Angulare, *De.* Dentale, *Psp.* Postspleniale, *Sp.* Spleniale, *C. a.* Commissura anterior, *S. so.* Sulcus supraorbitalis, *F. l.* Flexura lacrimalis, *S. io.* Sulcus infraorbitalis, *F. j.* Flexura jugalis, *S. j.* Sulcus jugalis, *S. a.* Sulcus articularis, *S. acc.* Sulcus articularis accessorius, *S. d.* Sulcus dentalis, *S. m.* Sulcus marginalis.

Supratemporale, Dermosupraoccipitale und Postorbitale wuchern gleichmässig nach allen seiten hin, ihre Umrisse unverändert bewahrend und deren Indexe verändern sich kaum in Abhängigkeit von den Schädeldimensionen. Die unerheblichen Schwankungen der Zahlen (s. deren Indexe) lassen sich hier durch individuelle Varianten in der Knochenform erklären.

Der Index des Tabulare nimmt mit dem Alter auf Kosten des Wachstums dessen Ausläufers nach-rückwärts zu.

Die Knochen der Seitenpartie des Schädels — das Jugale und Squamosum — wachsen mehr in die Breite.

Das Jugale bei *Benthosaurus* besitzt eine ringförmige Zone des intensiven Wachstums, die, wie es die Messungen erwiesen haben, ein Vorherrschen des Wachstums in die Breite über demjenigen in die Länge ergibt; das Squamosum hat dagegen eine fächerartige Zone des intensiven Wachstums, die mit der grösseren Anzahl ihrer Kämme lateralwärts und mit der kleineren nach vorne gerichtet ist.

Demnach berechtigen uns die Messungen folgende Schlussfolgerungen zu ziehen:

1. Die Präorbitalregion des Benthosaurus-Schädels wächst sehr rapide in die Länge.

2. Die Knochen der Postorbitalregion vergrössern ihr Areal gleichmässig nach allen Seiten.

3. An den Knochen des Seitenteils der Postorbitalregion wird ein unerhebliches Wachstum in die Breite verzeichnet.

Die Anwesenheit der Zone des intensiven Wachstums in der Präorbitalregion des Schädels von *Benthosaurus* bedingt eine sehr interessante Erscheinung. In den Sammlungen des paläozoologischen Instituts ist ein Exemplar eines jungen *Benthosaurus* (Nr. 4-19-2224) vorhanden, dessen Schädel 27,5 mm beträgt, während bei dem erwachsenen *Benthosaurus*, in Anbetracht einiger Kieferfragmente, der Schädel wahrscheinlich eine Länge von 700 mm erreichte. Bei der Erforschung des Schädels dieses jugendlichen Exemplars haben wir in der Postorbitalregion eine rundwabige Skulptur nachgewiesen, während die Präorbitalregion das einfache Muster eines radial gestrichelten Knochens bewahrte (Abb. 15). Somit war in dem betreffenden Fall ein deutlicher Hinweis vorhanden, der vordere Schädelteil wäre von dem hinteren im Sinne einer Verwicklung der Knochenskulptur etwas zurückgeblieben. Dieses Zurückbleiben ist offenbar ein Ergebnis des Vorhandenseins in der Präorbitalregion des Schädels von *Benthosaurus* einer Zone des intensiven Wachstums (Abb. 6, A und B).

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Ein analoges Bild des Baues der Skulptur ist von Broili (1905—1906) bei einem jugendlichen Exemplar von *Cochleosaurus bohemicus* beschrieben. Hier, gleichwie bei dem jungen *Benthosaurus* ist die rundwabige Skulptur lediglich in der Präorbitalregion vorhanden. In der Präorbitalregion des *Cochleosaurus* dagegen sind die Knochen bloss mit radialen Furchen bedeckt. Es ist anzunehmen, dass bei *Cochleosaurus* die Zone des intensiven Wachstums sich in derselben Schädelpartie wie bei *Benthosaurus* belagert hatte. Demnach verlangsamt das intensive Wachstum anscheinend das Auftreten der rundwabigen Skulptur, während die frühe Differenzierung der Skulptur lediglich in denjenigen Schädelpartien zustande kommt, wo kein intensives Wachstum beobachtet wird.

Ausser der Zone des intensiven Wachstums sind die Furchen am Benthosaurus-Schädel, die als Anlagestelle der sog. „Schleimkanäle" dienten, von grossem Interesse. Die Funktion dieser Kanäle darf bislang nicht als endgültig geklärt gelten. Immerhin unterliegt es keinem Zweifel, dass dieses System der Kanäle am Kopfe eines von den Sinnesorganen darstellte; bei den Fischen ist es mit den Organen der Seitenlinie verbunden. In dem in Betracht kommenden Fall interessieren uns die morphologischen Besonderheiten der Furchen, die von dem System der Seitenlinie am Schädel der Stegocephalen bestehen geblieben waren.

Vom morphologischen Standpunkt aus sind die Schleimkanäle von ALLIS (1889, 1898, 1900) an Fischen, von ROY MOODIE (1908) an Stegocephalen, von SÄVE—SÖDERBERGH (1932—1933) an *Osteolepis macrolepidotus* und *Ichthyostegidae* erforscht worden.

Im paläontologischen Schrifttum kommen Hinweise in bezug auf eine Reihe Eigentümlichkeiten des Charakters der Furchen des Schleimkanals vor. So verzeichnet WIMAN (1914) eine sehr grosse Breite der Furche bei *Lyrocephalus curi* und sehr schmale und tiefe Furchen bei *Aphaneramma rostratum* WOODW. (aus der Trias Spitzbergens). Am häufigsten jedoch beschränken sich die Verfasser auf eine Beschreibung des Verlaufs der Furche des Kanals in ganz allgemeinen Zügen. So vergleichen BURMEISTER (1849) und v. MEYER (1856—1858) auf Grund der Tatsache, dass die Furchen des Kanals jede Orbita mit einem fast kompletten Ringe umgeben, das Gesamtbild der Furchen mit einer Brille. Späterhin begann man das Bild des Verlaufs des Kanals mit einer Lyra zu vergleichen. Letzterer Vergleich hatte sich dermassen in der paläontologischen Literatur eingebürgert, dass manche Autoren bei der Beschreibung des Verlaufs der Furchen des Schleimkanals bei verschiedenen Gattungen der Labyrinthodonten sich auf diesen Vergleich allein beschränken (FRAAS, 1913; WIMAN, 1914; O. ABEL, 1919).

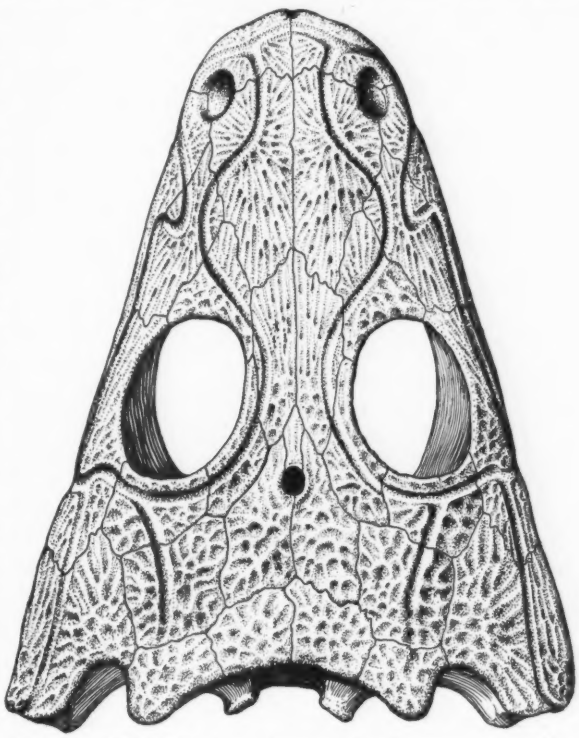

Abb. 15. Schädel eines jungen Benthosaurus sushkini. (Vergrössert um 3,5mal.) (Nr. 4-19-2224.)

Inwiefern es uns aus den Literaturangaben bekannt ist, hat sich mit der Erforschung der Beziehungen der Furchen des Schleimkanals zu den Schädelknochen noch niemand befasst; infolgedessen enthält das diesbezügliche Schrifttum bloss fragmentarische und akzidentelle Angaben. So verzeichnet WIMAN (1914) beiläufig, dass am Schädel von *Lyrocephalus curi* der „Temporalkanal" und „Maxillarkanal" in der Region des Ossifikationszentrums

des Jugale einsetzt. Dies ist der einzige Hinweis auf den Zusammenhang des Schleimkanals mit dem Ossifikationszentrum des Deckknochen des Schädels. Auf welche Weise sich der Schleimkanal den Ossifikationszentren der übrigen Knochen gegenüber verhält macht WIMAN keine Erwähnung.

MOODIE (1918), sich mit der Erforschung dieser Furchen bei Stegocephalen eigens befassend, lenkte sein Augenmerk ausschliesslich auf deren Vergleich mit den Schleimkanälen der *Crossopterygii,* indem er für diese Fische die Befunde von ALLIS verwertete. Die Beziehung aber dieser Furchen zu den einen oder anderen Schädelknochen des Stegocephalen liess er anscheinend ausser Acht. Infolgedessen ist in sämtlichen Fällen, wo MOODIE keine Kopie einer guten und richtigen Abbildung des Schädels aus den Arbeiten anderer Autoren dartut, die Beziehung der Furchen des Schleimkanals zu den Knochen von ihm falsch wiedergegeben.

Zwecks Klärung der Frage nach dem Verlaufe des Schleimkanals bei den Stegocephalen halten wir es für notwendig die Anordnung der entsprechenden Furchen am Schädel von *Benthosaurus sushkini* eingehend zu beschreiben. Wir werden dabei die heutzutage allgemein übliche Terminologie, die seinerzeit von MOODIE ausgebildet war, benutzen und lediglich das Schlagwort „Canalis" durch „Sulcus" ersetzen, da am Schädel bloss Furchen vorhanden sind, Kanäle aber als solche fehlen.

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An dem vorderen Ende der Schnauze des *Benthosaurus* lagert sich eine Furche, die von MOODIE als Commissura anterior bezeichnet war. Sie ist hier etwas länger, als es auf MOODIES schematischer Abbildung (1908, Fig. 1) dargestellt ist und verbindet die zentralen Zonen (die Regionen der rundwabigen Skulptur) des rechten und linken Praemaxillare. Beide Hälften dieser Furche stehen zueinander in einem Winkel von etwa 150°.

Die Commissura anterior erstreckt sich etwas nach hinten von dem Foramen interpraemaxillare und steht offenbar zu dieser Öffnung in keiner Beziehung (Abb. 16 — C. a.; F. i.).

An den Seitenrändern der Schnauzenspitze lässt die Commissura anterior eine sehr geringe Spur nach, doch ist es bei aufmerksamer Erforschung stets sichtbar, dass diese Furche in einen gut ausgeprägten Sulcus infraorbitalis übergeht (Abb. 12, 14 und 16 — S. 10.). An der Stelle, wo die Commissura anterior (C. a.) die zentrale Zone des Praemaxillare überschneidet, geht von ihr eine andere Furche — Sulcus supraorbitalis ab (Abb. 12 und 16 — S. so.). Diese Verbindung der Commissurae anterioris mit den Sulci supra- et infraorbitales verzeichnet MOODIE nicht, obschon sie zur genüge gut bei sämtlichen Labyrinthodonten ausgeprägt ist.

Es ist bemerkenswert, dass die Verbindungsstelle der Commissura und des Sulcus supraorbitalis ganz genau mit dem *Ossifikationszentrum* des Praemaxillare coinzidiert. Wie bekannt lässt sich dieses Zentrum mit Präzision an der etwas gestrichelten i n n e r e n Oberfläche eines beliebigen Deck-

knochens des Schädels des Stegocephalen definieren. In sämtlichen Fällen, wo die Furchen des Schleimkanals die zentralen Zonen dieser oder jener Schädelknochen durchkreuzen, erstrecken sie sich dabei stets vollkommen präzis a u c h über dem Ossifikationszentrum dieser Knochen (Abb. 1, A und B). Infolgedessen wäre es richtiger und präziser des weiteren, bei der Beschreibung des Verlaufs der Furchen in denjenigen Fällen, wo sie die Zentralzonen durchkreuzen, sich dahin zu äussern, dass deren entsprechende Bezirke das Ossifikationszentrum der betreffenden Knochen überschneiden. Die Erforschung dieser Frage an unserem Material hat erwiesen, dass solches in bezug auf sämtliche Knochen, auf deren zentralen Zonen die Furchen des Schleimkanals verlaufen, zutrifft.

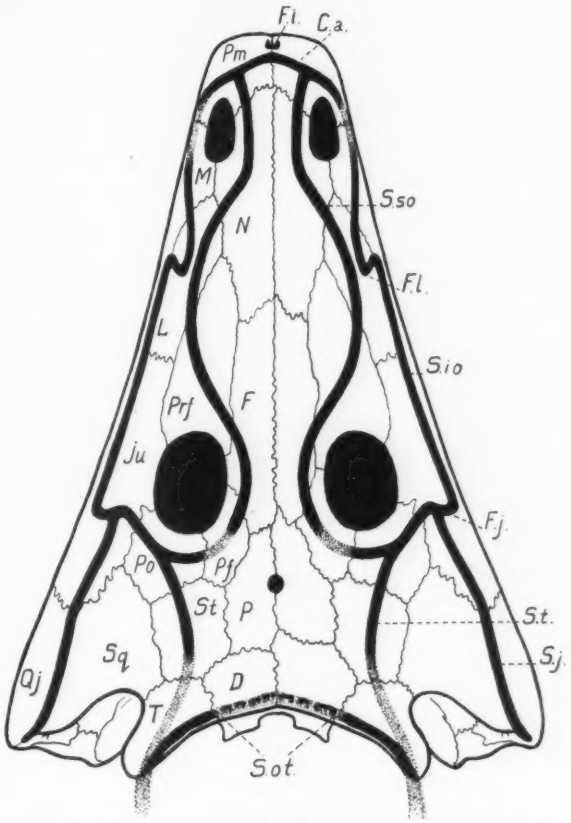

Abb. 16. Benthosaurus sushkini. *Pm.* Praemaxillare, *M.* Maxillare, *N.* Nasale, *L.* Lacrimale, *F.* Frontale, *Prf.* Praefrontale, *Ju.* Jugale, *P.* Parietale, *Pf.* Postfrontale, *Po.* Postorbitale, *St.* Supratemporale, *Sq.* Squamosum, *Qj.* Quadratojugale, *D.* Dermosupraoccipitale, *T.* Tabulare, *F. i.* Foramen interpraemaxillare, *C. a.* Commissura anterior, *S. so.* Sulcus supraorbitalis, *F. l.* Flexura lacrimalis, *S. io.* Sulcus infraorbitalis, *F. j.* Flexura jugalis, *S. t.* Sulcus temporalis, *S. j.* Sulcus jugalis, *S. ot.* Sulcus occipitalis transversus.

Der Verlauf des Sulcus infraorbitalis (Abb. 12, 14, 16 — S. io.) ist ziemlich kompliziert. Angefangen von der das Praemaxillare und Maxillare trennenden Naht gelangt diese Furche gut zum Ausdruck und richtet sich zu dem Ossifikationszentrum des Maxillare (Abb. 14). Weiterhin erreicht der Sulcus infraorbitalis, die Sutur zwischen Maxillare und Lacrimale in schräger Richtung überschneidend, die zentrale Zone des Lacrimale und bildet hier eine starke Krümmung, die wir als Flexura lacrimalis canalis infraorbitalis bezeichnen (Abb. 14 und 16 — F. l.). Das Knie der Krümmung wendet sich vom Ossifikationszentrum des Lacrimale lateralwärts und etwas

nach vorne und greift auf die Sutura maxillolacrimalis über. Von hier erstreckt sich der Sulcus infraorbitalis erst der erwähnten Naht entlang, geht sodann auf das Jugale über und erreicht das Ossifikationszentrum dieses Knochens (Abb. 14). Hier bildet der Sulcus infraorbitalis (S. io.) eine zweite Krümmung, die von uns als Flexura jugalis bezeichnet wird (F. j.). Das Knie dieser Krümmung ist medialwärts und etwas nach vorne gerichtet. Am Ende des Knies zerteilt sich die Furche in zwei Äste. Der eine von ihnen, der von MOODIE als Canalis jugalis (besser Sulcus jugalis) benannt war, zieht fast wagerecht längs dem Jugale (Abb. 14 und 16 — S. j.) und lagert sich sodann der Sutur zwischen Squamosum und Quadratojugale entlang. Am hinteren Schädelrande biegt sich der Sulcus jugalis etwas ventralwärts um und lässt sich auf einer gewissen Strecke längs des hinteren Randes des Quadratojugale verfolgen. Diese Krümmung weist anscheinend darauf hin, dass der Canalis jugalis sich mit dem System der Kanäle des Unterkiefers in Verbindung setzt (Abb. 14). Bei *Osteolepis macrolepidotus* (SÄVE—SÖDERBERGH, 1933) reicht das Ende des Canalis jugalis dermassen nahe an den Kanal des Unterkiefers, dass deren Vereinigung bei dem lebenden Fische keinem Zweifel unterliegt (Abb. 17 A). Bei den rezenten *Dipnoi* (GOODRICH, 1930) geht der Canalis jugalis in den Canalis mandibularis über. Es ist anzunehmen, solches hätte auch bei den Stegocephalen stattgefunden.

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Der zweite Ast — Sulcus temporalis (Canalis temporalis nach MOODIE; Canalis postorbitalis nach GOODRICH) (Abb. 12 und 16 — S. t.) richtet sich medialwärts und nach hinten und erreicht das Ossifikationszentrum des Postorbitale. Hier zerteilt sich der Sulcus temporalis in zwei der Länge nach ungleiche Äste. Der lange Ast wendet sich von dem Postorbitale nach rückwärts und gelangt zum Ossifikationszentrum des Supratemporale; der kurze reicht am häufigsten bloss an die Sutur zwischen Postorbitale und Postfrontale und findet hier seinen Abschluss. Es wäre anzunehmen, dass der Schleimkanal sich hinter der Augengrube mit dem Canalis supraorbitalis vereinigt, doch lässt in der Mehrzahl der Fälle diese Verbindung keine zur genüge deutliche Furche an der Schädelskulptur nach. Immerhin ist es an einigen Schädeln des *Benthosaurus,* sowie an Schädeln anderer Spezies der Labyrinthodonten zu ersehen, dass die Enden der beiden Kanäle sich vermöge eines Streifens breiterer und tieferer Waben verbinden (*Lonchorhynchus Öbergi* — WIMAN, 1914; *Metoposaurus diagnosticus* — FRAAS, 1889—1890). Bei *Dwinosaurus* (Abb. 29 und 30) umgeben beide Kanäle die Augengrube hinten mit einer kontinuierlichen Furche.

Der lange Ast des Sulcus temporalis (Abb. 16 — S. t.), nachdem er das Ossifikationszentrum des Supratemporale erreicht hat, setzt sich bei *Benthosaurus* gewöhnlich nicht fort. Bei *Aphaneramma rostratum* (WIMAN, 1914) reicht er an die Naht zwischen dem Supratemporale und Tabulare (Abb. 18 B); bei *Lyrocephalus euri* und *Lonchorhynchus Öbergi* überschneidet

er diese Naht und endet am Tabulare (Abb. 18 A u. C); dasselbe wurde von uns am Schädelfragment von *Trematosaurus Brauni* beobachtet (Abb. 18 D). Unseres Erachtens unterliegt es keinem Zweifel, der Canalis temporalis stehe bei dem lebenden Labyrinthodonten mit Canalis occipitalis transversus, dessen Furche längs dem hinteren Schädelrande verläuft, in Verbindung (Abb. 16 — S. o. t.). Dies ist umso mehr unzweifelhaft, da eine derartige Verbindung auch bei den Fischen (*Crossopterygii, Dipnoi*) statthat.

Der Sulcus occipitalis transversus (S. o. t.) ist bei *Benthosaurus* relativ schwach ausgeprägt. Deutlicher gelangt er bei alten Exemplaren des *Benthosaurus* und gut bei *Trematosaurus Brauni* zum Ausdruck (Abb. 25). Diese Furche bildet einen Bogen, der sich längs dem hinteren Rande der Dermosupraoccipitalia und Tabularia erstreckt. Vom langgezogenen hinteren Ende des Tabulare ging der in dieser Furche liegende Kanal wahrscheinlich, in den Schleimkanal des Rumpfes über. Somit erscheint es als wahrscheinlich, dass der Schleimkanal des Rumpfes bei den Stegocephalen an dem Gipfel des Tabulare entsprang und namentlich dort, wo der Sulcus occipitalis transversus und Sulcus temporalis miteinander verschmolzen (Abb. 16).

Burmeister (1849) hat bei der Darstellung des Schädels von *Trematosaurus Brauni* einen Irrtum begangen, indem er den Sulcus temporalis an die Incisura oticalis reichen liess. In der Folge wurde Burmeisters Irrtum von einer Reihe Autoren wiederholt, die Schemen des Verlaufs des Schleimkanals an Schädeln der Labyrinthodonten beigebracht haben. So bringt Fraas (1889—1890) auf seiner Abbildung des Schädels von *Mastodonsaurus giganteus*, gleichwie Burmeister, den Sulcus temporalis nicht bis zum Gipfel des Tabulare, sondern bis zu Incisura oticalis. Späterhin wiederholt Moodie (1908) in einer der Erforschung des Verlaufs des Schleimkanals bei den Stegocephalen gewidmeten Arbeit die Irrtümer von Burmeister und Fraas. Bis zur Incisura oticalis ist diese Furche bei Moodie auch auf der Abbildung des Schädels von *Metoposaurus diagnosticus* gebracht, obschon in Anbetracht des vorzüglichen Lichtdrucks, der in der Arbeit von Fraas den Metoposaurus-Schädel in Naturgrösse wiedergibt und von Moodie verwertet war, dazu keine Gründe vorliegen. Wiman (1917), die Rekonstruktion des Schädels von *Tertrema acuta* darstellend, beendigt den Sulcus temporalis gleichfalls am Rande der Incisura oticalis.

Der Sulcus supraorbitalis (Abb. 12, 16 — S. so.) nimmt seinen Anfang von der Commissura anterior (C. a.), an der Stelle, wo letztere das Ossifikationszentrum des Praemaxillare überschneidet. Von hier greift der Sulcus supraorbitalis, die Nasenlöcher medial umbiegend, auf das Ossifikationszentrum des Nasale über. Danach wendet er sich lateralwärts, kreutz in der Querrichtung die Sutura nasolacrimalis und erreicht die Zentralzone des Lacrimale. Hier lagert sich der Sulcus supraorbitalis in nächster Nähe des Sulcus infraorbitalis (S. io.). Moodie verbindet diese beiden Furchen vermöge

einer Kommissur, die er als Commissura anteorbitalis bezeichnet. Eine derartige Verbindung haben wir an dem uns zu Gebote stehenden Material kein einziges Mal beobachtet. Der Sulcus supraorbitalis wird im Bereiche der Zentralzone des Lacrimale vom Sulcus infraorbitalis gewöhnlich vermöge eines schmalen, jedoch stets zur Genüge gut ausgeprägten Kamms getrennt, dessen Oberfläche mit einer Reihe kleiner runden Grübchen bedeckt ist. Die Commissura anteorbitalis Moodie existiert bei den Labyrinthodonten wahrscheinlich überhaupt nicht.

Im weiteren Verlaufe erreicht der Sulcus supraorbitalis (S. so.), einen Bogen bildend, das Ossifikationszentrum des Praefrontale. Sodann, die Orbita von der medialen Seite umrahmend, richtet sich diese Furche zu dem Ossifikationszentrum des Frontale um schliesslich in der Region des Ossifikationszentrums des Postfrontale zu schwinden.

In Anbetracht der Literaturangaben sind die von dem System der Schleimkanäle am Unterkiefer der Stegocephalen belassenen Furchen eigens von niemand erforscht worden.

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Moodie (1908) berührt sie in seiner Arbeit nur beiläufig. Er hat die Abbildung bloss einer Furche des Canalis operculomandibularis am Unterkiefer von *Diplocaulis magnicornis* Cope gebracht. Ein mehr detailliertes Bild gibt Williston (1914) bei der Beschreibung des Unterkiefers von *Trimerorhachis allani* Case. Der Verlauf der Furchen ist bei *Trimerorhachis* und *Benthosaurus* vollkommen identisch. Williston unterscheidet zwei Grundfurchen: den Sulcus dentalis und Sulcus marginalis. Diese Bezeichnungen behalten auch wir bei unserer Beschreibung des Unterkiefers des *Benthosaurus* bei.

Die Hauptfurche des Unterkiefers des *Benthosaurus* beginnt am Supraangulare, etwas von dem Kiefergelenke zurückweichend. Wir bezeichnen sie sie als Sulcus articularis (Abb. 14 — S. a.). Diese Furche, ohne an den Rand des Angulare zu reichen, zerteilt sich in den Sulcus dentalis (S. d.) und Sulcus marginalis (S. m.).

Der Sulcus dentalis (S. d.) bildet einen schwach konvexen Bogen, längs der das Angulare vom Dentale trennenden Sutur verlaufend. Sodann erstreckt er sich geradlinig dem Dentale entlang bis dicht an das Ossifikationszentrum dieses Knochens am vorderen Ende des Unterkiefers, wo er in der rundwabigen Skulptur zum Schwunde kommt.

Der Sulcus marginalis (S. m.) erstreckt sich nach dem Kieferwinkel, der durch das Ossifikationszentrum des Angulare gebildet wird und greift späterhin auf die unter-innere Oberfläche des Unterkiefers über. Da die auf dieser Kieferoberfläche liegenden Knochen der Skulptur ermangeln, so gelingt es nicht den weiteren Verlauf des Sulcus marginalis zu verfolgen.

Der Sulcus articularis (S. a.) bei *Benthosaurus* besitzt noch einen Ast. Letzterer entspringt etwa in der Mitte des Sulcus articularis und, sich nach vorne richtend, tritt mit dem Sulcus dentalis in Vereinigung. Anfangs ist

diese supplementäre Furche stets gut ausgeprägt, gegen Ende gelangt sie weitaus schlechter zum Ausdruck. Ihrer ganzen Ausdehnung nach liegt sie im Bereiche des Supraangulare; wir bezeichnen sie als Sulcus articularis accessorius (Abb. 14 — S. acc.).

Die Erforschung der Furchen des Schleimkanals am Benthosaurus-Schädel legt uns folgenden Schluss nahe. Die Furchen erstrecken sich gewöhnlich entweder längs der Sutur zwischen zwei angrenzenden Knochen oder überschneiden das Ossifikationszentrum dieses oder jenes Knochens. Letzteres kommt ungleich häufiger vor. Diese Erscheinung lässt sich höchstwahrscheinlich folgendermassen erklären. An den Schädeln der Larven der Stegocephalen, deren Knochen einer scharf ausgeprägten Skulptur noch verlustig waren, werden keine Furchen des Schleimkanals beobachtet. Die Furchen gelangen zum Ausdruck bloss nach dem Auftreten des Waben- und Kämmesystems. Immerhin unterliegt es keinem Zweifel, dass bei den Kiemenatmenden und im Wasser lebenden Larven das System der Schleimkanäle hinreichend gut entwickelt war. Die Deckknochen des Schädels stellen in diesem frühen Entwicklungsstadium, wie es CREDNER am *Branchiosaurus amblistomus* nachgewiesen hat, sehr geringfügige Gebilde dar. Zweifelsohne entsprechen diese primären Larvenknochen denjenigen Teilen der Schädelknochen der erwachsenen Stegocephalen, die wir als „zentrale Zonen" bezeichnen. Die kleinen Schädelknochen der Larve berühren sich gegenseitig mit ihren Rändern und bilden den Schädelkasten aus; der Schleimkanal liegt ihnen auf. Bei dem weiterem Wachstum des Schädels wachsen nicht sämtliche Deckknochen, ihr Areal regelmässig nach allen seiten erweiternd, — einige von ihnen wuchern in gewisser Richtung mehr intensiv. Dies alles modifiziert letzten Endes die Gesamtkonfiguration des Schädels. Allerdings bleibt der Schleimkanal mit denjenigen primären Knochenanlagen in Verbindung, die den Larvenschädel zusammensetzten. Da jedoch die primären Anlagen der Schädelknochen der Larve den Ossifikationszentren der Knochen der erwachsenen Stegocephalen entsprechen (Region der rundwabigen Skulptur), so müssen die Furchen des Schleimkanals an den Schädeln der erwachsenen Stegocephalen die sog. „zentralen Zonen" durchziehen. Dieser Zusammenhang zwischen dem Ossifikationszentrum und dem Verlaufe des Schleimkanals lässt sich vermutlich durch die Stabilität des Verhaltens der Nervenäste den Knochenelementen des Schädels gegenüber erklären. Bei den rezenten Fischen wird das System der Schleimkanäle an dem Kopfe durch den N. facialis innerviert. Dieser Nerv innervierte wahrscheinlich die betreffenden Kanäle auch bei den Stegocephalen. Dessen feinste Äste, bevor sie sich in den Kanalwandungen verästelten, durchbohrten den Knochen, was auch bei den rezenten Fischen beobachtet wird. An *Benthosaurus* ist bei guter Erhaltung der Schädel, auf dem Boden einer jeden Furche des Kanals eine Menge feiner Öffnungen sichtbar (Abb. 3). Einige

von diesen Öffnungen dienten anscheinend als Austrittsstellen der feinen Äste des N. facialis, andere — als ebensolche Stellen für Blutgefässe. Im Laufe der Knochenwucherung konnten die Grundäste des N. facialis ihre Beziehungen zu den primären Anlagen der Schädelknochen nicht modifizieren und hatten sie nicht modifiziert. Solches aber bedingte wiederum die Stabilität der Beziehungen des Schleimkanals zu den Ossifikationszentren, da dessen Lage gänzlich von den Ästen des ihn innervierenden Nerven abhängig war. Im Wachstumsvorgange eines jeglichen Knochens nahm die Länge des in der Furche an der Knochenoberfläche liegenden Schleimkanals zu und dieses beeinflusste den Verlauf der feinen Äste des N. facialis. Diejenigen unter ihnen, die präzise das Ossifikationszentrum überschnitten, hatten ihren senkrechten Verlauf im Knochen beibehalten, während die übrigen, ohne ihren Zusammenhang mit dem sich verlängernden Schleimkanal einzubüssen, eine schräge Stellung erworben hatten. Als Ergebnis werden auf der Strecke eines jeden Abschnitts der Furche am beliebigen Knochen Mündungen schmaler s e n k r e c h t e r Kanäle dort, wo die Furche das Ossifikationszentrum kreuzt, und s c h r ä g e r Kanäle in den vom Ossifikationszentrum entfernten Bezirken der Furche beobachtet (Abb. 3).

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Einige Bezirke der Furchen des Schleimkanals an den Schädeln der Stegocephalen verlaufen längs der Naht zwischen dem einen oder dem anderen Paar der Deckknochen. So erstreckt sich die caudale Hälfte des Sulcus jugalis bei *Benthosaurus* der Naht entlang zwischen dem Squamosum und Quadratojugale; ein Teil des Sulcus infraorbitalis zwischen der Flexura lacrimalis und Flexura jugalis zieht sich ebenfalls längs der das Lacrimale und Maxillare trennenden Naht; schliesslich lagert sich zuweilen der Sulcus dentalis auf einer gewissen Ausdehnung längs der Naht zwischen dem Dentale und Angulare (Abb. 14). In den übrigen Fällen verlaufen die Furchen des Schleimkanals vom Ossifikationszentrum eines Knochens bis zum Ossifikationszentrum eines anderen.

Eine aufmerksame Erforschung dieser drei Fälle des eigenartigen Verlaufs der Furchen hat erwiesen, dass deren Verlauf längs der Naht zwischen den angrenzenden Knochen als eine sekundäre Erscheinung zu betrachten ist. Die Sache ist nämlich die, dass das Quadratojugale als ein Knochen in der Totalität weitaus grösser ist, als es von der äusseren Schädeloberfläche den Anschein hat. Es besitzt einen grossen und flachen Ausläufer, der nach oben zieht und unter das Squamosum reicht. Somit erweist sich der caudale Teil des Sulcus jugalis total im Bereiche des Quadratojugale gelegen. Das intensiv lateralwärts und nach vorne wachsende Squamosum, den oberen Rand des Quadratojugale bedeckend, reicht bloss an die Furche. Inwiefern es uns bekannt ist, empfängt lediglich bei einer Gattung der Labyrinthodonten — bei *Trematosaurus Brauni* — der Rand des Squamosum auf seine Oberfläche beim weiteren Wachstum einen gewissen Bezirk des Canalis jugalis; infolge-

dessen durchzieht die Furche des Kanals in Gestalt eines unerheblichen Bogens quer über die Zone des intensiven Wachstums dieses Knochens.

Was den Bezirk des Sulcus infraorbitalis anbelangt, so liegt er im wesentlichen am Maxillare, da der obere Rand dieses Knochens in der in Betracht kommenden Stelle von dem Lacrimale bedeckt ist.

Eine gleiche Besonderheit sehen wir auch in der Naht zwischen dem Angulare und Dentale. Bei Erforschung der Schnitte des Unterkiefers von *Benthosaurus* hat es sich herausgestellt, dass ein beträchtlicher Bezirk des hinteren Abschnitts dieses Knochens von aussen mit dem kräftig gewucherten Rande des Angulare bedeckt ist, so dass die Naht zwischen diesen Knochen das Gepräge der Sutura squamosa trägt. Der Sulcus dentalis, obschon er längs dem Rande des Angulare verläuft, ist hier auf seiner ganzen Ausdehnung im Bereiche des Dentale, etwa in einer gleichen Entfernung von dessen oberem und unterem Rande gelagert.

Die Naht zwischen dem Angulare und Supraangulare stellt ebenfalls keine Sutura dentata, sondern Sutura squamosa dar und, reichte das Angulare mit seinem Rande an die Gabelungsstelle des Sulcus articularis in den Sulcus dentalis und Sulcus marginalis, so hätte sich die gesamte hintere Hälfte des Sulcus dentalis als längs der Naht verlaufend erwiesen.

Somit erstrecken sich die Furchen bloss in den Fällen der Naht entlang, wo kraft der Ausbildung der Sutura squamosa der Rand eines Knochens sich auf den Rand eines anderen legend, knapp an diesen oder jenen Bezirk der Furche des Schleimkanals reicht.

In diesem Falle stellt es sich heraus, dass der Schleimkanal bei den Stegocephalen lediglich mit den Ossifikationszentren der Deckknochen des Schädels verbunden ist und dass sein Verlauf längs einiger Suturen eine sekundäre Erscheinung darstellt.

Sehr interessante Eigentümlichkeiten in Verlaufe des Sulcus jugalis werden bei den von Watson (1921, 1924, 1926) beschriebenen Stegocephalen des Unterkarbons beobachtet. So überschneidet bei *Palaeogyrinus decorus* (Abb. 17 C) und *Eugyrinus wildi* die Furche des Schleimkanals, in Anbetracht der Abbildungen des Verfassers, das Ossifikationszentrum des Squamosum, was bei geologisch mehr frühzeitigen erwachsenen Stegocephalen gewöhnlich nicht beobachtet wird. Bei *Palaeogyrinus decorus* ergibt die das Ossifikationszentrum des Squamosum überschneidende Furche einen halbkreisförmigen Ast, der nach unten und rückwärts gerichtet ist und dem Quadratojugale aufliegt. Es wäre anzunehmen, dass gegebenenfalls der in der Furche am Squamosum angelegte Kanal sich mit demjenigen Aste des Canalis infraorbitalis verband, der die Augengrube von hinten umbiegt. Letzterer Kanal beliess am Schädel von *Palaeogyrinus* eine zur Genüge gut ausgeprägte Furche. Die soeben erwähnte Verbindung der Kanäle ist von uns auf Abb. 17 C mit punktierten Linien verzeichnet. In diesem Falle stellt die Furche

am Squamosum bei *Palaeogyrinus decorus* ein Homologon des Sulcus jugalis bei *Benthosaurus sushkini* und bei den anderen Labyrinthodonten späterer Perioden dar.

An einer sehr interessanten Form — *Ichthyostegopsis wimani* — die aus den Ablagerungen des Devons Grönlands gewonnen war und vor kurzem von SÄVE-SÖDERBERGH (1932) beschrieben ist, ist es gut zu ersehen, dass ein gleicher Schleimkanal, wie es bei den Stegocephalen aus dem Karbon der Fall war, am Squamosum verläuft (Abb. 17 B). Ausserdem ist es an den Präparaten von SÄVE-SÖDERBERGH vollkommen evident, dass dieser Kanal das Ossifikationszentrum des Squamosum überschneidet und sich mit dem Canalis infraorbitalis in der Region des Ossifikationszentrums des Jugale vereinigt. SÄVE-SÖDERBERGH verzeichnet das Vorhandensein bei *Ichthyostegopsis wimani* eines unerheblichen Schleimkanals, der sich längs dem Quadratojugale erstreckt (Canalis quadratojugalis). Dieser Kanal ist vermutlich demjenigen am Quadratojugale bei *Palaeogyrinus decorus* homolog.

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Nach SÄVE-SÖDERBERGH sind die *Ichthyostegidae* ein Seitenzweig im Stammbaume der Stegocephalen, welch ersterer sich noch im mittleren Devon abgesondert hatte und im oberen bereits ausgestorben war. Immerhin steht diese Form ihrer Struktur nach den gemeinsamen Vorfahren der Stegocephalia zweifellos sehr nahe. Was den Verlauf des Schleimkanals am Schädel einer derartigen Form wie *Ichthyostegopsis wimani* anbelangt, so ist der Gang des Kanals einigen Besonderheiten zufolge der Anordnung des gleichen Gebildes bei den karbonischen Stegocephalen sehr ähnlich.

Von nicht geringerem Interesse in betreff auf den Verlauf des Schleimkanals ist auch *Osteolepis macrolepidotus*, als ein fossiler Vertreter der *Crossopterygii* aus dem Devon, mit welchen gewöhnlich die Ausgangsformen der Vorfahren der Stegocephalia verknüpft werden. Bei diesem Fisch, in Anbetracht des von SÄVE-SÖDERBERGH (1933) vorzüglich abpräparierten und beschriebenen Exemplars, überschnitt der Canalis jugalis, gleichwie bei den Ichthyostegidae und den Stegocephalen aus dem Karbon, das Ossifikationszentrum des Squamosum (Abb. 17 A). Dies drängt uns zur Annahme, die soeben besprochene Eigentümlichkeit stelle ein sehr altertümliches Merkmal dar.

WIMAN (1914—1917) hat bei der Beschreibung des Schädels von *Tertrema acuta* aus der Trias Spitzbergens eine interessante Eigentümlichkeit im Verlaufe des Sulcus temporalis verzeichnet. Diese Furche zerspaltet sich beim Übergange von dem Ossifikationszentrum des Postorbitale auf das Ossifikationszentrum des Supratemporale in drei gesonderte Äste und durchkreuzt die Naht zwischen den obigen Knochen. Eine gleiche Eigentümlichkeit beobachten wir auch an dem von I. A. EFREMOV (1932) beschriebenen *Trematosaurus Brauni* aus dem Berge Bogdò (Abb. 18 D). Bei den anderen Gattungen der Stegocephalen aus der Trias Spitzbergens beschreibt

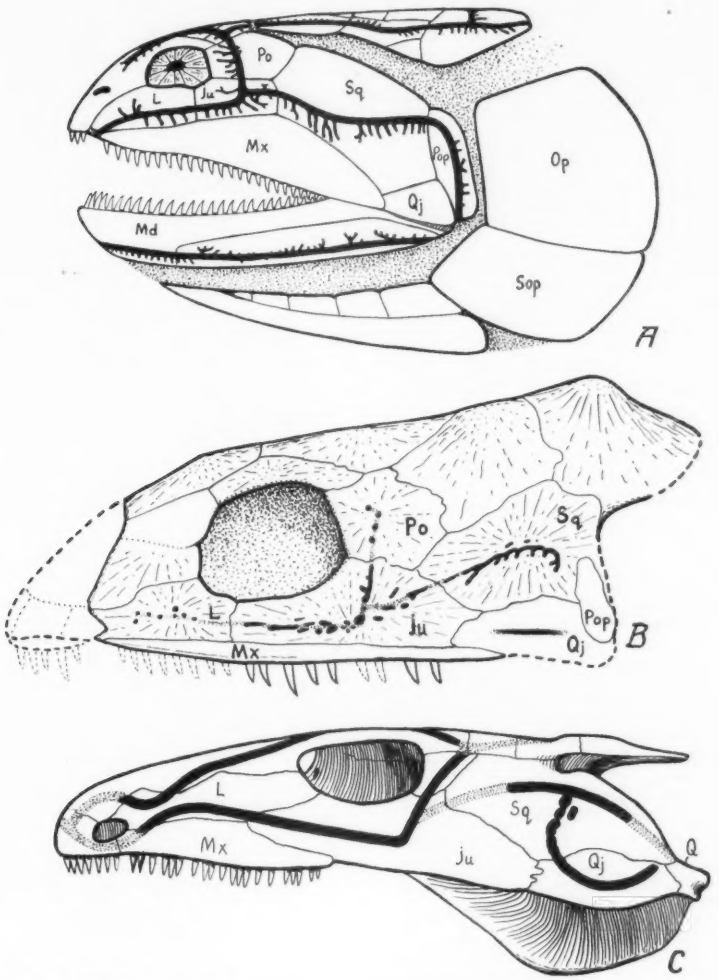

Abb. 17. *A* Osteolepis macrolepidotus, *B* Ichthyostegopsis wimani (nach Säve-Söderbergh), *C* Palaeogyrinus decorus (nach Watson).

Wiman (1914) eine Reihe sog. „Anomalien" im Verlaufe des Schleimkanals. So biegt sich an einem Exemplar von *Lonchorhynchus Öbergi* (Abb. 18 C) die Furche des Schleimkanals am linken Postorbitale mit seinem Ende nach vorne und endigt in der Region des Ossifikationszentrums des Postfrontale; am rechten Postfrontale ist die entsprechende Furche mit ihrem Ende caudalwärts gerichtet und reicht fast an den Rand des Supratemporale. Eine etwas andersartige „Anomalie" findet bei *Aphaneramma rostratum* (Abb. 18 B) statt. Hier entsendet an der rechten Seite der Sulcus temporalis im Bereiche des Postorbitale eine unerhebliche Abzweigung, die mit ihrem Ende caudal-

wärts gerichtet ist; an der linken Seite ist der von dem Sulcus temporalis abgetrennte halbkreisförmige Bezirk der Furche des Schleimkanals ebenfalls mit seinem Ende nach rückwärts gerichtet, doch ist er zur Hälfte im Bereiche des Postfrontale gelagert und darf nicht als ein dem linken entsprechendes Gebilde gelten. Diese beiden Furchen treten mit den Enden des Sulcus supraorbitalis nicht in Verbindung. Bei *Lyrocephalus euri* (Abb. 18 A) sind an beiden Seiten kleine Äste vorhanden, die von den Sulci supraorbitalis abgehen, die Sutur zwischen dem Postfrontale und Supratemporale kreuzen und den Sulci temporales parallel verlaufen. Der in dieser Furche liegende Schleimkanal verband sich wahrscheinlich in der Region des Ossifikationszentrums des Supratemporale mit dem Haupttemporalkanal, ergab jedoch keinen deutlichen Abdruck an der Skulptur der äusseren Knochenoberfläche (s. punktierte Linie auf Abb. 18 A). Bei *Lyrocephalus* ist es gut zu ersehen, dass der Sulcus temporalis in der Region des Postfrontale direkt in den Sulcus supraorbitalis übergeht. Bei *Lonchorynchus Öbergi, Tertrema acuta, Trematosaurus Brauni, Aphaneramma rostratum* und manchen anderen Labyrinthodonten ist zwischen den erwähnten Furchen am Postfrontale eine Unterbrechung vorhanden. Hier rief der Bezirk der Schleimkanals offenbar keine Ausbildung der Furche hervor; immerhin liegen keine Gründe vor dessen Existenz zu bezweifeln. Auf unserer Abbildungen (Abb. 18) ist dieser Bezirk mit punktierten Linien bezeichnet. Was den kleinen Ast am rechten Postfrontale bei *Lonchorhynchus* (C) anbetrifft, so ist es anzunehmen, der Schleimkanal wäre hier, gleichwie bei *Lyrocephalus* mit dem Canalis temporalis in der Region des Ossifikationszentrums des Supratemporale verbunden. Dieser supplementäre Kanal (Abb. 18 — C. t. a. — Canalis temporalis accessorius) des *Lonchorhynchus* entspricht dem linken supplementären Kanal des *Aphaneramma* (B), da diese Kanäle in beiden Fällen sich vom Ossifikationszentrum des Postfrontale zum Ossifikationszentrum des Supratemporale erstrecken. Der supplementäre Kanal an der rechten Hälfte des Schädels von *Aphaneramma* ist kein dem supplementären Kanal der linken Seite homologes Gebilde. Auf unserer Abbildung (Abb. 18), die ein Schädelfragment von *Aphaneramma* darstellt, ist das komplette Bild des Verlaufs der Schleimkanäle rekonstruiert; dabei sind mit punktierten Linien diejenigen Bezirke der Kanäle verzeichnet, die sich am Schädel in Form von Furchen nicht abgedruckt hatten und durch einen schwarzen Streifen gut ausgeprägte Furchen wiedergegeben, die sich auf WIMANS Photoaufnahmen deutlich unterscheiden lassen. Auf dieser Abbildung ist der supplementäre Kanal der linken Seite auf die rechte übertragen und umgekehrt, da wir der Ansicht sind, die Zerspaltung des Canalis temporalis wäre wahrscheinlich symmetrisch gewesen. Demnach erweist es sich, dass bei *Aphaneramma* die Naht zwischen dem Postfrontale und Supratemporale von einem Kanal und die

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Naht zwischen dem Postorbitale und Supratemporale von zwei Kanälen überschnitten wird. Bei *Trematosaurus* (das von I. A. Efremov im Jahre 1932 beschriebene Exemplar) ist die Naht zwischen dem Postorbitale und Supratemporale nicht von zwei, sondern von drei Furchen durchkreuzt. Ausserdem biegt sich bei dieser Gattung der Sulcus supraorbitalis vom Ossifikationszentrum des Postfrontale caudalwärts um, so dass es anzunehmen wäre, der Schleimkanal dieser Furche reichte an das Ossifikationszentrum des Supratemporale, wo er mit dem Canalis temporalis in Verbindung trat (s. den punktierten Streifen auf Abb. 18 D). Somit ist an unserem Exemplar von Trematosaurus eine maximale Anzahl der Zerspaltungen des Canalis temporalis — vier Äste — vorhanden; drei derselben sind am Fragment sehr gut sichtbar.

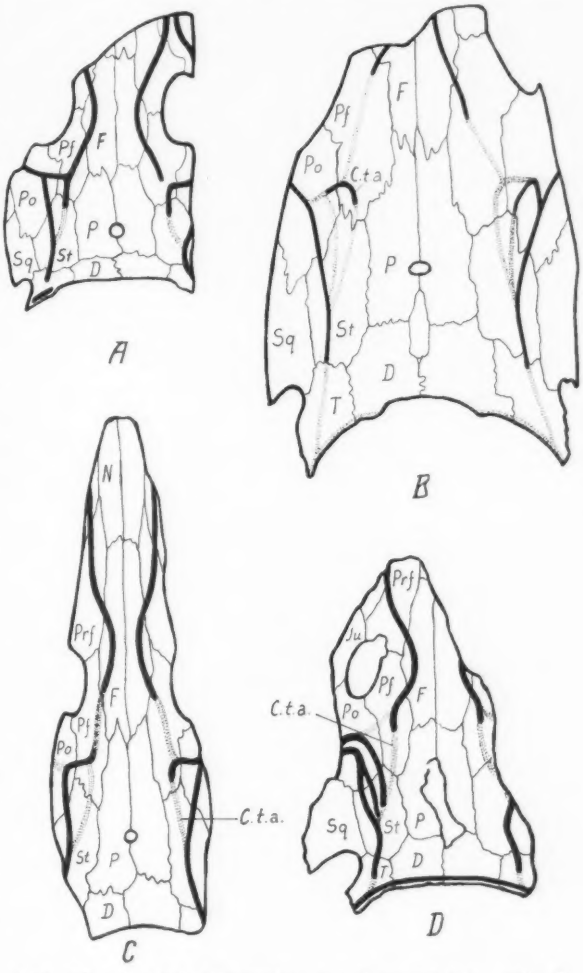

Abb. 18. *A* Schädelfragment von Lyrocephalis euri, *B* Schädelfragment von Aphaneramma rostratum, *C* Schädelfragment von Lonchorhynchus Öbergi (*A*, *B*, *C* nach Wiman), *D*. Schädelfragment von Trematosaurus Brauni; Nr. 3-2247-14. *C. t. a.* Canalis temporalis accessorius.

Die angegebenen Beispiele weisen darauf hin, dass der Schleimkanal bei den Labyrinthodonten sich in einigen Fällen in mehrere einander parallele Äste zu spalten vermag, ohne das Gesamtschema seines Verlaufes und dasjenige Verhalten den Ossifikationszentren der Deckknochen gegenüber, das wir bereits analysiert haben, zu stören. Die Ursachen dieser Verstärkung des Systems der Seitenlinie am Kopfe der Stegocephalen bleiben für uns bislang unaufgeklärt.

III.

Die Schädel einiger Stegocephalen besitzen nicht eine, wie *Benthosaurus sushkini*, sondern mehrere Zonen des intensiven Wachstums.

Der Anzahl dieser Zonen zufolge teilen wir sämtliche Stegocephalen (die Zonen besitzen) in drei Gruppen ein. Jede von diesen Gruppen zerfällt wiederum je nach der Lage der Zone (resp. Zonen) im Schädel in mehrere Typen. Ausserdem schälen wir noch eine vierte Gruppe heraus, der wir diejenigen Gattungen der Stegocephalen zurechnen, deren Schädel überhaupt keine Zone des intensiven Wachstums besitzt.

Gruppe I.

Die erste Gruppe umfasst Stegocephalen, in deren Schädel eine Zone des intensiven Wachstums vorhanden ist. Je nach der Lage dieser Zone zerfallen die Stegocephalen der ersten Gruppe in drei Typen.

Typus 1. Dem ersten Typus gehören Stegocephalen an, deren einzige Zone des intensiven Wachstums in der hintersten Schädelpartie, namentlich zwischen dem Foramen parietale und dem Occipitalrande gelegen ist. Einer derartige Anordnung der Zone begegnen wir bei relativ altertümlichen Stegocephalen aus dem oberen Karbon und dem unteren Perm.

Als gutes Beispiel des ersten Typus der ersten Gruppe kann *Diceratosaurus punctolineatus* Cope (Jaekel, 1903) dienen; seine Schädellänge beträgt 35 mm.

Bei diesem Stegocephalen (Abb. 19) sind das Postorbitale, Supratemporale, Tabulare und Squamosum anscheinend sehr früh miteinander verschmolzen, indem sie einen grossen Knochen mit sehr mächtiger Zone des intensiven Wachstums zustande gebracht hatten. Dieser komplexe Knochen, wie es die Skulptur an dessen Oberfläche erweist, wucherte sehr kräftig nach vorne gegen die Orbita und rückwärts, hier ein grosses Horn bildend; weitaus schwächer wuchs er lateralwärts. Die Skulptur der Oberfläche derartiger Deckknochen, wie das Dermosupraoccipitale und Parietale, zeigt, dass sie gleichmässig, doch zur Genüge intensiv nach allen Seiten wuchsen. Als Folge eines derartigen Knochenwachstums nahm diejenige Schädelpartie, die hinter dem Foramen parietale gelegen ist, beträchtlich zu und wucherte caudalwärts. Bei den Labyrinthodonten lagert sich das Foramen parietale gewöhnlich im Niveau der Ossifikationszentren der Parietalia. Bei *Diceratosaurus punctolineatus* ist es ins vordere Drittel der Parietalia verschoben, was darauf hinweist, die Parietalia und die hinter ihnen liegenden Dermosupraoccipitalia wären im Wachstumsvorgange nach rückwärts verlagert.

Die Anordnung des Foramen parietale im vorderen Drittel der Naht zwischen dem Paar der Parietalia betrachtet Jaekel (1903) als Merkmal der

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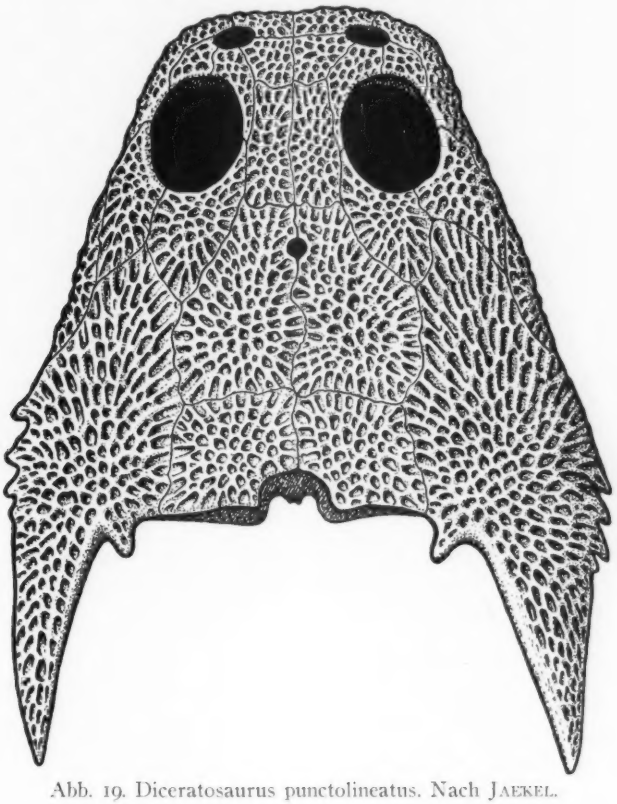

Abb. 19. Diceratosaurus punctolineatus. Nach JAEKEL.

Primitivität des *Diceratosaurus*. Unseres Erachtens ist in dem entsprechenden Fall nicht die Lage des Foramen parietale, sondern diejenige der Zone des intensiven Wachstums hinter dieser Öffnung primitiv.

Bei den fossilen (*Osteolepis macrolepidotus*) und rezenten (*Polypterus bichir*) *Crossopterygii* sind die die präorbitale Schädelregion zusammensetzenden Knochen klein, während das Areal eines jeden, in der postorbitalen Region liegenden Knochens ungleich grösser ist. Das gleiche sehen wir im Grunde auch am Schädel von *Diceratosaurus punctolineatus*. Eine Reihe von Deckknochen, die dessen Augen- und Nasenlöcher umrahmen, stellen unerhebliche, mit runden Waben bedeckte Gebilde dar, was auf ein Fehlen des intensiven Wachstums hinweist. Bei *Benthosaurus*, wie bereits erwähnt, wuchern die in den Bereich der Zone des intensiven Wachstums geratenen Knochen der Schädeldecke gewöhnlich sehr kräftig, am häufigsten in einer gewissen Richtung. Bei *Diceratosaurus* vergrössern die in der Wachstumszone liegenden Knochen intensiv ihr Areal fast gleichmässig nach allen Seiten. In diesem Sinne weisen sie mit den Knochen der postorbitalen Region

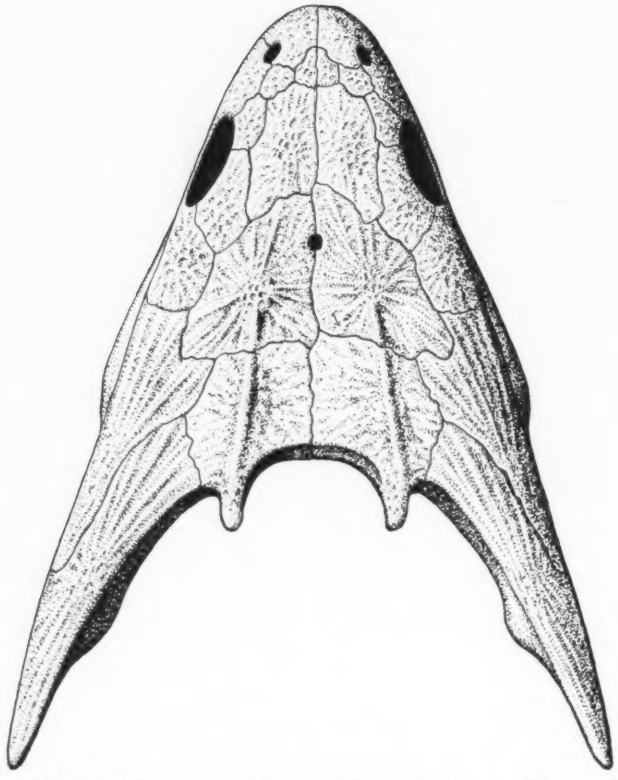

Abb. 20. Batrachiderpeton lineatum. Rekonstruktion nach den von WATSON beschriebenen Fragmenten.

der Crossopterygii sehr grosse Ähnlichkeiten auf. Somit besitzt *Diceratosaurus* eine primitive Zone des intensiven Wachstums sowohl deren Lage nach, als auch dem Charakter selbst des Wachstums der sie zusammensetzenden Knochen zufolge.

Dem ersten Typus der ersten Gruppe ist auch der Schädel von *Batrachiderpeton lineatum* HANC. et ATTH., aus dem Oberkarbon zuzurechnen (WATSON, 1913) (Abb. 20).

In Anbetracht der Dimensionen der Schädelknochen lässt sich mit Sicherheit behaupten, dass die Zone des intensiven Wachstums sich auch bei dieser Gattung hinter dem Foramen parietale lagert. Hier sind die Knochen ungleich grösser, als in der vorderen Schädelpartie. Die Oberfläche der die Zone des intensiven Wachstums bildenden Knochen ist bei *Batrachiderpeton* nicht von wabiger, sondern von radialer Skulptur. Die vom Ossifikationszentrum radial auseinanderweichenden langen Kämme sind dabei entsprechend der Richtung des Knochenwachstums orientiert. Von den im Bereiche der Zone des intensiven Wachstums liegenden Knochen ist lediglich

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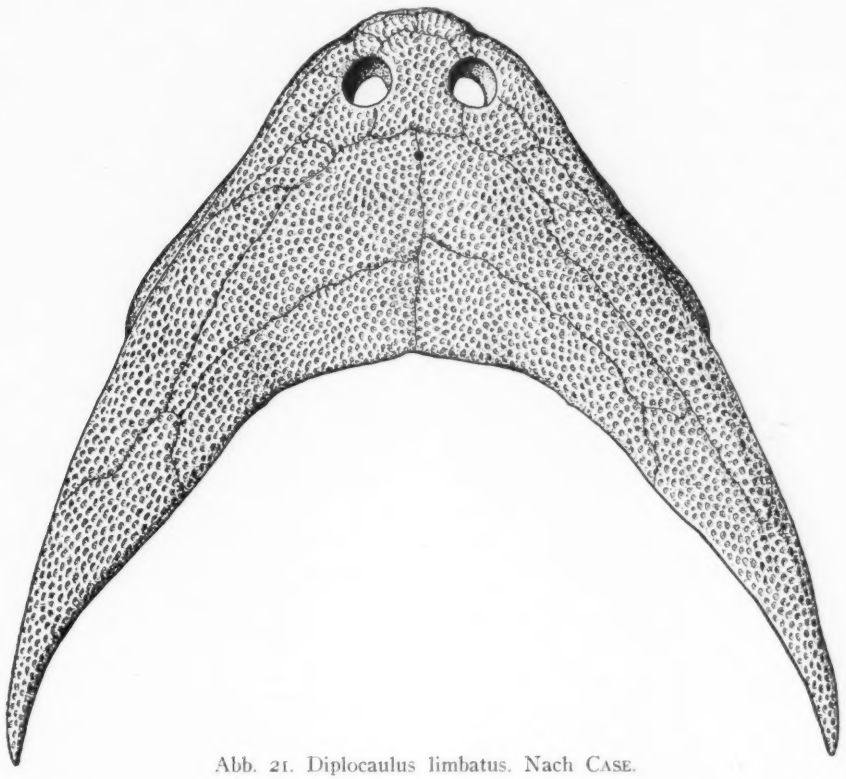

Abb. 21. Diplocaulus limbatus. Nach CASE.

am Parietale das Auftreten im Ossifikationszentrum von runden Waben angedeutet. Im Gegenteil ist die rundwabige Skulptur an der Oberfläche derartiger Knochen wie Frontale, Post- und Praefrontale, Lacrimale und Nasale zur Genüge gut ausgeprägt. Bei *Batrachiderpeton* haben wir offenbar mit derselben Erscheinung, auf die wir bereits bei jugendlichen Exemplaren von *Benthosaurus sushkini* und *Cochleosaurus bohemicus* zu stossen kamen, zu tun. Und zwar: die Differenzierung der Skulptur verspätet sich gewissermassen in der Region der Zone des intensiven Wachstums. Bei *Benthosaurus* (jugendliches Exemplar, Abb. 15) bleibt die rundwabige Skulptur in der präorbitalen Region aus, bei *Batrachiderpeton* fehlt sie an der Mehrzahl der Knochen der postpinealen Schädelpartie. Diese Besonderheit der Skulptur an der Knochenoberfläche und der relativ geringe Schädelumfang (etwa 75 mm) drängt uns den von WATSON beschriebenen Schädel des *Batrachiderpeton lineatum* als einem sehr jungen Tiere zugehörigen zu betrachten, welches kaum die Kiemenatmung durch Lungenatmung ersetzt hatte. Das Vorhandensein der runden Waben an den Knochen der vorderen Schädelpartie weist offenbar darauf hin, dass die Metamorphose bei dem in

Betracht kommenden Exemplar bereits ihren Abschluss gefunden hatte, das Ausbleiben einer deutlich ausgeprägten Wabenskulptur in der hinteren Partie zeugt von dessen relativer Jugend.

Die Schädel der Stegocephalen aus dem unteren Perm — *Diplocaulus magnicornis* Cope und *Diplocaulus limbatus* (Abb. 21), können ebenfalls dem ersten Typus der ersten Gruppe zugerechnet werden.

Die Zone des intensiven Wachstums bei *Diplocaulus* liegt zweifelsohne in der postpinealen Schädelpartie. Der Diplocaulus-Schädel ist wie bekannt von sichelförmiger Gestalt; das Foramen parietale, die Augen- und Nasenlöcher sind bei dieser Spezies in die Nähe des vorderen stumpfen Schnauzenrandes verdrängt; der Hinterhauptsteil des Schädels ist nach rück- und seitwärts in Form zwei grosser und spitzer Hörner gewachsen. Entsprechend der Form des Schädels sind auch die ihn bildenden Deckknochen in die Länge gestreckt. Immerhin weist deren Skulptur, trotz des zweifellosen kräftigen Wachstums der Knochen nach hinten und seitwärts, keine Bezirke mit einem für die Zonen des intensiven Wachstums charakteristischen Relief auf. Sämtliche Schädelknochen sind mit gleichen kreisförmigen Waben bedeckt; Kämme, welche von uns z. B. bei *Benthosaurus* beschrieben waren, sind hier an keinem einzigen Knochen vorhanden.

Zwecks Klärung dieser interessanten Eigentümlichkeit wandten wir uns zur Erforschung jugendlicher Exemplare den Beschreibungen von Broili (1904—1905) zufolge. Es stellte sich heraus, dass Schädel der jungen Diplocaulus (70 mm Länge der Mittellinie nach) Gesamtumrisse besitzen, die den Schädelumrissen der alten identisch sind (150 mm Länge). Die Skulptur der Schädelknochen von jugendlichen *Diplocaulus* weicht keineswegs von der Skulptur der erwachsenen ab — die Knochen sind durchwegs lediglich mit runden Waben bedeckt. Somit bleiben die für die Zone des intensiven Wachstums kennzeichnenden Kämme bei den jüngern Vertretern des *Diplocaulus* aus. Das weist darauf hin, dass *Diplocaulus* sehr früh eine eigenartige Schädelform erhielt, die im Laufe des ganzen Lebens des Tieres bestehen blieb. Das intensive Wachstum einiger Schädelknochen schloss die Ausbildung der Schädelausmasse offenbar noch im Larvenstadium ab. Im Augenblick des Verlustes der Kiemen hatte der Diplocaulus-Schädel bereits eine für diesen Stegocephalen charakteristische Form. Des weiteren, im Vorgange der Metamorphose oder nach derselben bedeckte die rundwabige Skulptur die Gesamtoberfläche der Schädelknochen. Bei dem nachfolgenden Wachstum blieben die Umrisse des Schädels, trotz dessen Zunahme ums doppelte, unverändert, demnach wuchs jeder Schädelknochen gleichmässig nach allen Seiten und wurde in den neugebildeten Bezirken mit der üblichen Wabenskulptur bedeckt. Somit besitzen wir an *Diplocaulus*, bei primitiver Lage der Zone des intensiven Wachstums (in der postpinealen Schädelpartie) anscheinend eine arteigene spezialisierte Form,

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bei welcher die Schädelausbildung bereits im Larvenstadium der Entwicklung ihren Abschluss gefunden hatte und die weitere Zunahme der Dimensionen des Schädels vermöge des üblichen Wachstums der ihn bildenden Knochen vor sich ging.

Ein kleiner Schädel des Stegocephalen aus dem Karbon — *Eoserpeton tenuicorne*, der von MOODIE (1909) beschrieben worden ist, besass in Anbetracht der schematischen Abbildung dieses Autors, eine Zone des intensiven Wachstums zwischen dem Foramen parietale und dem Hinterhauptsrande und ist demselben Typus der ersten Gruppe, gleichwie *Diceratosaurus* und *Batrachiderpeton* zuzurechnen.

Typus 2. Bei den Stegocephalen des zweiten Typus der ersten Gruppe liegt die Zone des intensiven Wachstums des Schädels zwischen dem Foramen parietale und den Orbiten.

Ein gutes Beispiel dieses Typus stellt der grosse Labyrinthodont aus der oberen Trias — *Metoposaurus diagnosticus* H. VON MEYER, dar (Abb. 22). Die Länge seines Schädels beträgt 450 mm. Die Skulptur der Deckknochen des Schädels weist deutlich darauf hin, dass das Tabulare und Dermosupraoccipitale keine Zonen des intensiven Wachstums besitzen; sie sind durchweg von runden Waben bedeckt und haben relativ geringe Dimensionen. Den soeben erwähnten Knochen liegen knapp die zentralen Zonen des Parietale, Supratemporale und Squamosum an. Die sehr kräftigen Zonen des intensiven Wachstums dieser Knochen sind nach vorne gerichtet. Das Squamosum wuchs ausser nach vorne auch

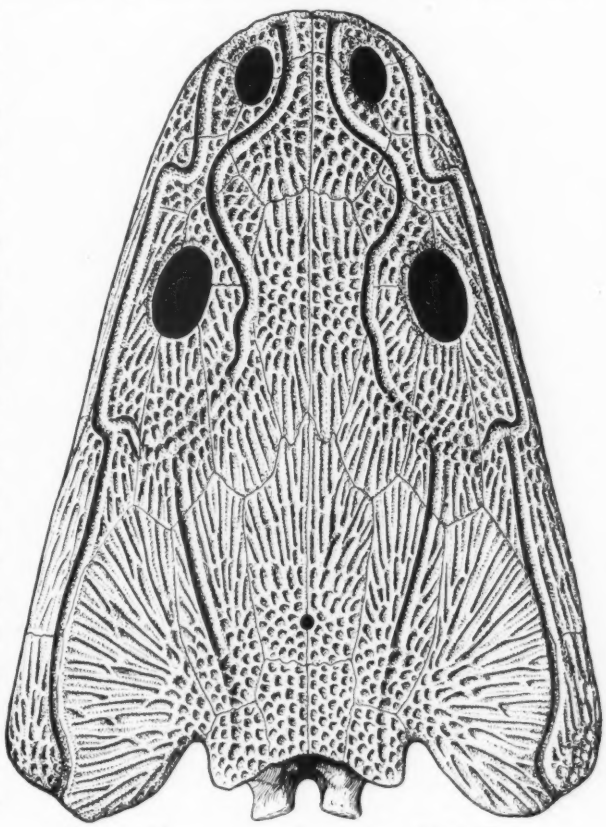

Abb. 22. Metoposaurus diagnosticus. Nach FRAAS.

lateralwärts. Nach vorne ist auch das Wachstum des Quadratojugale gerichtet. Unerhebliche Zonen des intensiven Wachstums sind auch an den Hinterenden des Frontale, Postfrontale, Postorbitale und Jugale vorhanden.

Als Ergebnis einer derartigen Anordnung der Wachstumszonen der einzelnen Knochen setzt sich am Schädel von *Metoposaurus diagnosticus* eine Gesamtzone des intensiven Wachstums zusammen, die quer über dem Schädel zwischen dem Foramen parietale und den Orbiten gelegen ist. Diese Zone hatte die Verlagerung der Augenlöcher in die vordere Schädelpartie, näher zu den Nasenlöchern bedingt.

Eine gleiche Anordnung der Zone des intensiven Wachstums ist auch am Schädel von *Anaschisma brown*i vorhanden.

Typus 3. Als Beispiel des dritten Typus der Anordnung der Zone des intensiven Wachstums wollen wir den Schädel des Labyrinthodonten aus der oberen Trias — *Cyclotosaurus* verwerten (Abb. 23). Die Länge seines Schädels beträgt 530 mm.

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Bei *Cyclotosaurus* liegt die Zone des intensiven Wachstums zwischen den Orbiten und den Nasenlöchern. Sie ist durch das intensive Wachstum des Frontale, Praefrontale, Jugale nach vorne und des Nasale, Lacrimale nach hinten bedingt. Die Skulptur an der äusseren Knochenoberfläche im Bereiche der Zone ist durch gut ausgeprägte lange Kämme dargestellt. Die soeben besprochene Anordnung der Zone des intensiven Wachstums hat ein Hervorragen des vorderen Schnauzenendes mitsamt den Nasenlöchern nach vorne bewirkt. Die Orbiten und das Foramen parietale sind in der hinteren Schädelpartie bestehen geblieben. Die mit rundwabiger Skulptur bedeckten zentralen Zonen der gesonderten Knochen sind bei *Cyclotosaurus* im vorderen und hinteren Schädelbezirke konzentriert. Eine interessente Besonderheit des *Cyclotosaurus* ist das Vorhandensein der Zone des intensiven Wachstums am Ende des Tabulare. Als Folge war das Tabulare mit dem nach rückwärts gewucherten Squamosum in Verbindung getreten und die Incisura oticalis hatte sich in Foramen oticale umgewandelt. Das Squamosum besitzt bei *Cyclotosaurus,* wie bei sämtlichen Stegocephalen eine eigene konstante Zone des intensiven Wachstums. Das Wachstum dieses Knochens lateralwärts bedingt die Zunahme der hinteren Schädelpartie in die Breite. Das Postfrontale, Postorbitale, Parietale, Supratemporale und Dermosupraoccipitale stellen bei *Cyclotosaurus* verhältnismässig kleine Knochen dar, die durchweg mit runden Waben bedeckt sind und keine Zonen des intensiven Wachstums besitzen.

Die Labyrinthodonten *Cyclotosaurus* und *Metoposaurus,* wie bereits erwähnt, gehören der Lage der Zone des intensiven Wachstums in ihren Schädeln gemäss zwei verschiedenen Typen an. Immerhin existierten diese beiden Spezies in der oberen Trias, gelangten zu sehr grossen (und fast

gleichen) Dimensionen, besitzen sehr ähnliche (fast identische) Gesamtumrisse des Schädels und gehören schliesslich dem Bau der Wirbelsäule nach den *Steriospondyli* an. Infolgedessen ist der Vergleich der Besonderheiten im Aufbau ihrer Schädel, welch erstere ausschliesslich durch die verschiedene Lage der Zonen des intensiven Wachstums bedingt sind, von grossem Interesse. Das Foramen parietale und die Nasenlöcher bei *Metoposaurus* und *Cyclotosaurus* behaupten eine gleiche Lage im Schädel. Dagegen sind die Augenlöcher bei *Metoposaurus* in die vordere, bei *Cyclotosaurus* in die hintere Schädelpartie verdrängt. Trotz der verschiedenen Lagen jedoch sind sie in beiden Fällen durch gleichnamige Knochen — des Prae- und Postfrontale, Postorbitale und Jugale begrenzt. Als eine bei den Stegocephalen ziemlich selten vorkommende Ausnahme ist an der Bildung der Orbiten bei *Cyclotosaurus* auch das Frontale beteiligt.

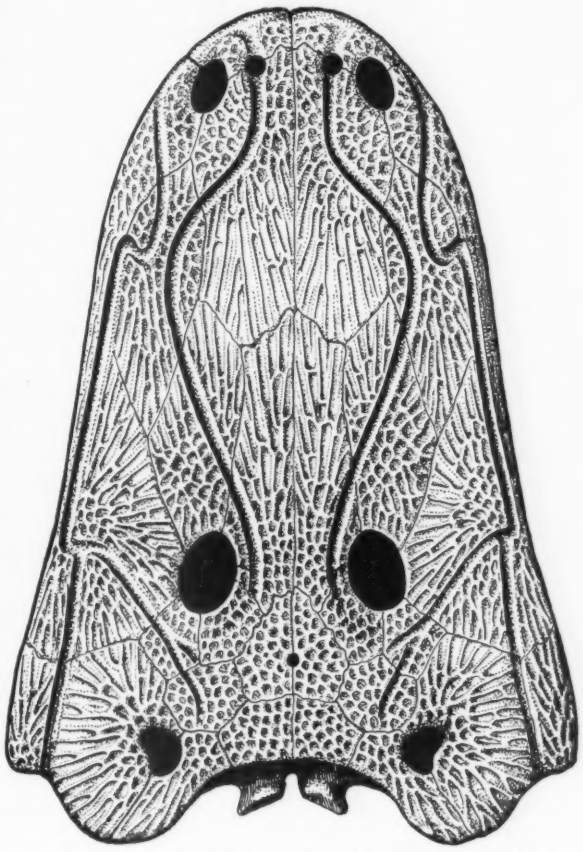

Abb. 23. Cyclotosaurus. Rekonstruktion nach den Materialien von FRAAS.

Aus dem Vergleich der beiden Schädel erhellt, dass die Orbiten ihre Lage mitsamt dem Komplex der sie umrahmenden Knochen verändern. Dabei bleiben die zentralen Zonen der Frontalia, Praefrontalia, Postfrontalia und Postorbitalia stets in unmittelbarer Nähe zu den Orbiten bestehen.

Es ist bereits bei der Beschreibung des Verlaufs der Furchen der Schleimkanäle bei *Benthosaurus sushkini* die Konstanz des Zusammenhangs dieser Kanäle mit den zentralen Zonen, präziser gesagt, mit den Ossifikationszentren der Deckknochen des Schädels erwähnt worden. Am Beispiel von *Metoposaurus* und *Cyclotosaurus* wird diese Eigentümlichkeit der Kanäle

vollkommen bestätigt. Bei dem Vergleiche der Furchen des Schleimkanals an den Schädeln dieser beiden Spezies von Labyrinthodonten wird sofort augenfällig, dass der Schleimkanal, ohne sein Verhältnis zu den Ossifikationszentren zu modifizieren, das Gesamtbild seines Verlaufs im Falle der Veränderung der Lage im Schädel derjenigen Knochen, mit denen er gewöhnlich verbunden ist, modifiziert.

Von hervorragendem Interesse ist die Tatsache, dass die mannigfaltigen Lagen der Zone des intensiven Wachstums bei *Metoposaurus* und *Cyclotosaurus,* die Verlagerungen der Orbiten und Veränderungen im Gesamtbilde des Verlaufs der Furchen des Schleimkanals bewirken, sich keineswegs an der Struktur der Schädelbasis wiedergespiegelt haben (Abb. 34). Die Struktur der Basis cranii ist bei diesen beiden Gattungen fast identisch.

Der Lage der einzigen Zone des intensiven Wachstums im Schädel zufolge sind dem dritten Typus der ersten Gruppe, ausser *Cyclotosaurus* und *Benthosaurus* noch folgende Stegocephalen zuzurechnen: *Wetlugosaurus, Mastodonsaurus giganteus, Capitosaurus* (untere Trias), *Archegosaurus Decheni, Cochleosaurus bohemicus* (unteres Perm) und einige andere.

In Anbetracht der zur Zeit im Schrifttum vorhandenen Materialien ist der dritte Typus der Anordnung der einzigen Zone des intensiven Wachstums bei den Stegocephalen der am meisten verbreitete.

Gruppe II.

An den Schädeln einiger Stegocephalen lassen sich nicht eine, sondern zwei Zonen des intensiven Wachstums ermitteln. Derartige Stegocephalen rechnen wir der zweiten Gruppe zu. Je nach der Anordnung im Schädel zweier Wachstumszonen sind die Stegocephalen der zweiten Gruppe in drei Typen einzuteilen.

Typus 1. Dem ersten Typus gehören Stegocephalen an, in deren Schädel beide Zonen des intensiven Wachstums im postorbitalen Gebiete liegen. Dabei lagert sich eine derselben zwischen dem Foramen parietale und dem Hinterhauptsrande des Schädels, die andere zwischen dem Foramen parietale und den Orbiten.

Eine derartige Anordnung zweier Zonen des intensiven Wachstums ist bei dem Stegocephalen aus dem Unter-Karbon *Dolichopareias disjectes,* der von Watson (1926) beschrieben worden ist, vorhanden.

Watson bringt keine Darstellung der Skulptur der Dermalknochen dieser Spezies bei, infolgedessen sind wir nicht imstande die Anordnung der Ossifikationszentren und der Wachstumszonen der einzelnen Knochen in der in Betracht kommenden postorbitalen Schädelregion genau festzustellen. Doch

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schreibt WATSON, dass „All the dermal bones of the skull bear an ornament of pits, ridges and grooves, of the type which is so common in Labyrinthodont skulls". Das berechtigt uns zur Annahme, alle charakteristischen Eigentümlichkeiten, denen wir gewöhnlich bei sämtlichen Stegocephalen im Bereiche der Zone des intensiven Wachstums begegnen, wären auch bei *Dolichopareias disjectes* vorhanden.

Am Schädel von *Dolichopareias* haben sich Spuren des Schleimkanals lediglich an drei Knochen erhalten. Diese Knochen bezeichnet WATSON als Supratemporale, Squamosum und Dermosupraoccipitale. In Anbetracht seiner Abbildung (Fig. 27, S. 249 — Abb. 24 A) setzen die Furchen des Kanals an dieser und jener Schädelseite am Supratemporale ein und gehen dann direkt auf das Squamosum über. Ein derartiger Verlauf der Furchen wurde bei keiner Spezies der Stegocephalen beobachtet. Von dem Supratemporale geht der Schleimkanal in der Regel auf das Tabulare, nicht aber auf das Squamosum über. Liegt dem Squamosum ein Bezirk des Schleimkanals auf, so greift er gewöhnlich auf diesen Knochen vom Jugale über, einen Teil des Canalis jugalis bildend. Von solcher Art ist der Verlauf des Canalis jugalis nicht bloss bei den primitiven Stegocephalen, sondern auch bei *Ichthyo-*

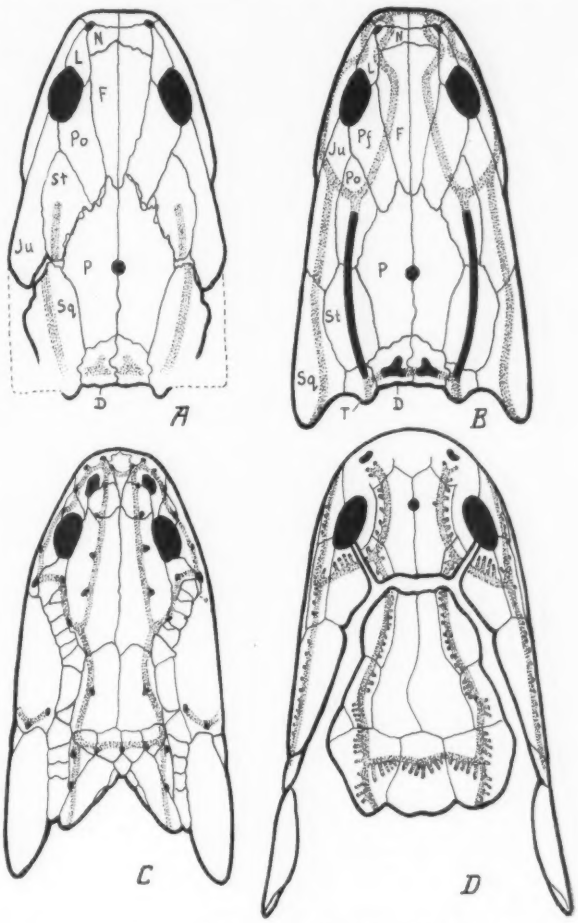

Abb. 24. *A* Dolichopareias disjectes (nach WATSON, Palaeontologica Hungarica, Fig. 27, S. 249), *B* Dolichopareias disjectes (Rekonstruktion des Verfassers), *C* Polypterus bichir (nach ALLIS), *D* Osteolepis macrolepidotus (nach SÄVE-SÖDERBERGH). *N.* Nasale, *F.* Frontale, *P.* Parietale, *D.* Dermosupraoccipitale, *St.* Supratemporale, *Po.* Postorbitale, *Pf.* Postfrontale, *Ju.* Jugale, *Sq.* Squamosum.

stegopsis und *Osteolepis*. Demnach, falls die zwei Stücke, aus denen von WATSON der Dolichopareias-Schädel zusammengestellt ist, tatsächlich einer Spezies angehören, so ist der auf Watsons Abbildung (Abb. 24 A) mit den Buchstaben Sq bezeichnete Knochen eher das Supratemporale, als das Squamosum. WATSON, der diesen Knochen als Squamosum betrachtet, äussert sich dahin aus: „The squamosal is produced into a small process in the usual position of a tabular horn." Am wahrscheinlichsten handelt es sich um ein kleines Tabulare, das mit dem Supratemporale verschmolzen war und einen Knochen (das Squamosum von WATSON) gebildet hatte. Wenn dem so ist, stellt der von WATSON als Supratemporale bezeichnete Knochen ein von der Orbita nach rückwärts verdrängtes Postorbitale dar. Somit ist die paarige Furche am Dolichopareias-Schädel eine Spur des Canalis temporalis, der vom Ossifikationszentrum des Postorbitale auf das Supratemporale, sodann auf das Tabulare übergeht, wo er mit dem Canalis occipitalis transversus, dessen Furche an den Dermosupraoccipitalia besteht, in Verbindung tritt. Ein andersartiges Verhältnis des Canalis temporalis zu den Schädelknochen ist bei den Stegocephalen nicht beobachtet worden; infolgedessen genügt das Vorhandensein am Dolichopareias-Schädel der Furche dieses Kanals vollkommen um die Bereichnung der Knochen, an welchen er sich hinzieht, genau festzustellen. Was fernerhin die Verschmelzung des Tabulare und Supratemporale anbelangt, so ist diese Eigentümlichkeit n i c h t ausschliesslich den *Dolichopareias* eigen. Bei *Diceratosaurus punctolineatus*, wie bereits erwähnt, war in derselben Schädelpartie eine noch grössere Anzahl der Schädelknochen verchmolzen.

Auf Abb. 24 ist neben der Kopie der Abbildung von WATSON (A) unsere Rekonstruktion (B) des *Dolichopareias disjectes* dargestellt, wobei einige Knochen anders benannt sind und ein Gesamtbild des Verlaufs des Schleimkanals gegeben ist, wie wir es uns auf Grund der Erforschung der Verhältnisse dieses Kanals zu den Schädelknochen vorstellen.

Die zwei Zonen des intensiven Wachstums haben die postorbitale Schädelpartie von *Dolichopareias* dermassen verlängert, dass die Gesamtumrisse seines Schädels sehr an denjenigen der Fische erinnern, z. B. *Polypterus bichir* von den rezenten und *Osteolepis macrolepidotus* von den fossilen (Abb. 24, C und D). Immerhin liegt das Foramen parietale bei *Osteolepis* zwischen den Frontalia, während es bei *Dolichopareias* zwischen den Parietalia — an der für sämtliche Stegocephalen typischen Stelle gelagert ist. Inwiefern es sich von einer Zone des intensiven Wachstums bei *Osteolepis* zu reden lässt, lagert sie sich bei ihm in der postpinealen Schädelpartie. In diesem Sinne dürfen mit *Osteolepis* die Stegocephalen des ersten Typus der ersten Gruppe und *Dolichopareias disjectes* verglichen werden, welch letzterer eine von den Zonen in der postpinealen Schädelpartie besitzt. Die andere Zone des intensiven Wachstums bei *Dolichopareias* liegt zwischen dem Foramen parietale

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und den Orbiten, was unanfechtbar von einem gewissen Grade der Spezialisierung dieser Gattung im Vergleich zu *Diceratosaurus punctolineatus, Batrachiderpeton lineatum, Diplocaulus limbatus et magnicornis* (erster Typus der ersten Gruppe) zeugt. Demnach ist bei *Dolichopareias* ausser dem Merkmal der Primitivität (postpineale Wachstumszone) auch das Merkmal einer gewissen Spezialisierung (präpineale Zone) vorhanden.

Vermutlich waren dem Typus der Anordnung der Zonen des intensiven Wachstums zufolge derartige Stegocephalen aus dem Karbon wie *Adelogyrinus simorhynchus* (WATSON, 1926), *Diceratosaurus robustus* und *Diceratosaurus levis* (MOODIE, 1909) dem *Dolichopareias disjectes* ähnlich.

Typus 2. Bei den Vertretern des zweiten Typus sind die zwei Zonen des intensiven Wachstums, im Vergleich zu *Dolichopareias disjectes,* nach vorne verdrängt. Eine von den Zonen lagert sich, wie bei *Dolichopareias* zwischen dem Foramen parietale und den Orbiten; die andere zwischen den Augen- und Nasenlöchern. Diesem Typus gehören *Trematosaurus Brauni* und *Tertrema acuta* an (WIMAN, 1914). Die Länge des Schädels von *Trematosaurus* beträgt 210 mm.

Die erste Zone bei *Trematosaurus Brauni* (Abb. 25) ist durch das intensive Wachstum der Vorderenden der Parietalia, Supratemporalia, Squamosa, Quadratojugalia und der Hinterenden der Frontalia, Postfrontalia, Postorbitalia und Jugalia bedingt. Diese zwischen dem Foramen parietale und den Orbiten querüber den Schädel gelegene Zone hat die Orbiten nach vorne verlagert. Die zweite Zone des intensiven Wachstums, die durch die gesteigerte Wucherung der Vorderenden der Frontalia, Praefrontalia, Jugalia und Hinterenden der Nasalia und Lacrimalia erzeugt war, hatte in derselben Richtung die Schnauzenspitze mitsamt den Nasenlöchern verschoben.

Der Verlauf der Furchen des Schleimkanals am Trematosaurus-Schädel ist gleichwie bei sämtlichen Stegocephalen der Anordnung der zentralen Zonen der Deckknochen vollständig untergeordnet. Deise zentralen Zonen gruppieren sich ringsum die Nasenlöcher an der Schnauzenspitze, um die Orbiten und in der Occipitalregion des Schädels hinter dem Foramen parietale. Die Furchen des Kanals sind entsprechend der Keilform des Schädels langgestreckt. Als eine interessante Besonderheit von *Trematosaurus* tritt, wie bereits erwähnt, die Spaltung des Sulcus temporalis in drei Äste bei dem Übergange dieser Furche von dem Ossifikationszentrum des Postorbitale auf das Ossifikationszentrum des Supratemporale hervor.

BURMEISTER (1849) beschreibt in seiner Abhandlung über *Trematosaurus* die Spaltung des Sulcus temporalis nicht. Als gesondert ist diese Furche auch auf den Schemen von MOODIE (1908) dargestellt. JAEKEL (1909) bringt eine Abbildung, auf welcher der Sulcus temporalis in zwei Äste zerteilt ist. An dem uns zu Gebote stehenden und von I. A. EFREMOV (1932) als

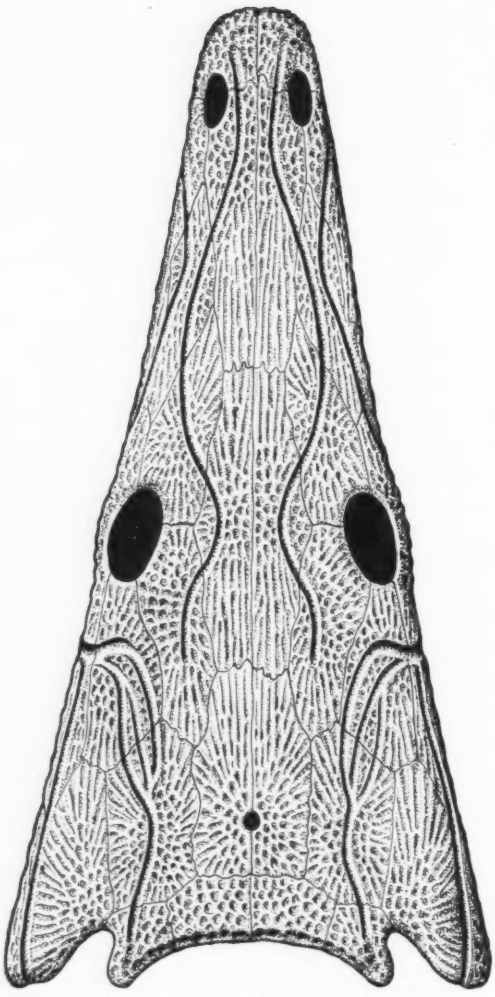

Abb. 25. Trematosaurus brauni. Rekonstruktion nach den Materialien von Burmeister und den Fragment des Paläozoologischen Instituts (Nr. 3-2247-14).

Fragment des *Trematosaurus Brauni* beschriebenen Schädelfragment ist der Sulcus temporalis in drei Äste gespaltet (Abb. 18 D).

Wiman (1914—1917) hat bei der Erforschung der fragmentarischen Reste von *Tertrema acuta* bei diesem Labyrinthodonten im Bereiche des Postorbitale eine gleiche Spaltung des Sulcus temporalis in drei parallele Furchen nachgewiesen. *Tertrema acuta* ist in manchen Eigentümlichkeiten dem *Trematosaurus Brauni* sehr ähnlich. Der Anzahl und der Lage der Zonen des intensiven Wachstums zufolge gehört er demselben Typus wie *Trematosaurus* an. Die Zerteilung des Sulcus temporalis in drei Äste bringt deise beiden Gattungen noch näher zueinander. Es ist anzunehmen, dass falls die von Wiman beschriebenen Reste von *Tertrema acuta* keine Reste von *Trematosaurus Brauni* darstellen, diese beiden Spezies allerdings als einander sehr nahestehende Formen zu betrachten wären.

Typus 3. Bei den diesem Typus angehörigen Stegocephalen sind die Zonen des intensiven Wachstums folgendermassen angeordnet: die eine liegt zwischen den Orbiten und den Nasenlöchern, die andere zwischen den Nasenlöchern und dem vorderen Schnauzenrande. Diesem Typus sind die Labyrinthodonten aus Perm *Platyops stuckenbergi* und *Platyops watsoni* zuzurechnen, deren Schädelfragmente von I. A. Efremov (1933) beschrieben waren.

Der auf unserer Abbildung (Abb. 26) wiedergegebene Schädel von *Platyops watsoni* ist auf Grund der Erforschung einer ziemlich grossen Anzahl von

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Schädelfragmenten dieser Spezies rekonstruiert. Die Schädellänge beträgt etwa 300 mm.

Die Zone des intensiven Wachstums zwischen den Orbiten und den Nasenlöchern ist bei ihm durch das excessive Wachstum derselben Knochen, wie die entsprechende Zone von *Trematosaurus* bedingt (Vorderteile der Frontalia, Praefrontalia, Jugalia und Hinterteile der Nasalia, Lacrimalia). Die vor den Nasenlöchern liegende Zone ist durch die sehr kräftige Zunahme der Hinterränder lediglich eines paarigen Knochens des Praemaxillare bedingt. Die mit rundwabiger Skulptur bedeckten Knochenanteile sind bei *Platyops* in drei Schädelpartien konzentriert: 1) in der Orbital- und Postorbitalregion, 2) in der Nähe der Nasenlöcher und 3) an der Spitze der etwas erweiterten Schnauze. Die zwei in der Präorbitalregion gelagerten Zonen des intensiven Wachstums haben den Platyops-Schädel in einen zugespitzten und langen Keil mit Nasenlöchern umgewandelt, die fast in der Mitte der Strecke zwischen dem vorderen Schnauzenrande und den Orbiten angeordnet sind.

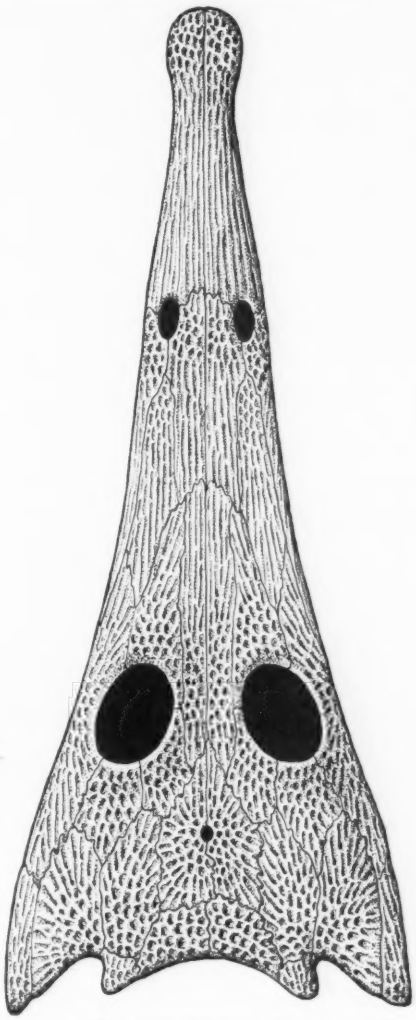
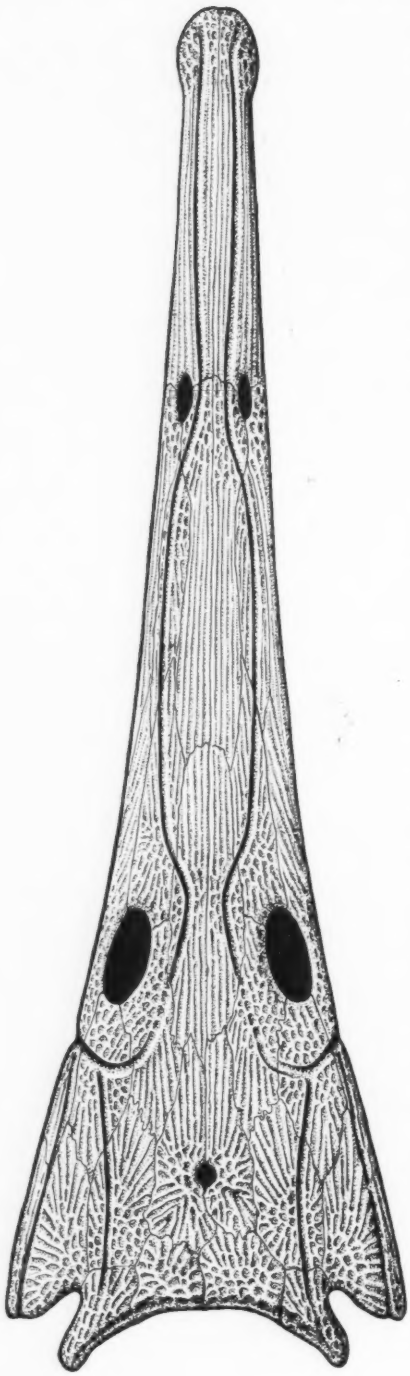


Abb. 26. Platyops watsoni. Rekonstruktion auf Grund der Fragmente der Paläozoologischen Instituts [Nr. 6, 15, 18, 19 (2250)].

Bei *Platyops* ist kraft irgendwelcher besonderen Gründe sichtbar eine fast komplette Reduktion des Systems der Schleimkanäle eingetroffen. Es gelang uns bloss sehr undeutliche Spuren von Einbuchtungen an einigen Anteilen der Dermalknochen des Schädels nachzuweisen und zwar lediglich bei den ältesten Exemplaren dieser Gattung.

Gruppe III.

Der dritten Gruppe gehören die Schädel derjenigen hochspezialisierten Labyrinthodonten an, bei denen drei Zonen des intensiven Wachstums



vorhanden sind. In Anbetracht einer derartigen Anzahl der Zonen ist die Möglichkeit der verschiedenen Kombinationen im Sinne deren Anordnung im Schädel selbstredend bei weitem verringert. Infolgedessen haben wir in der dritten Gruppe bloss einen Typus.

Typus 1. Ein gutes Beispiel eines Stegocephalen, dessen Schädel drei Zonen des intensiven Wachstums besass, ist unzweifelhaft der von WIMAN (1914) beschriebene *Lonchorhynchus Öbergi* aus der unteren Trias (Abb. 27). Seine Schädellänge beträgt ca. 320 mm.

Der auf Abb. 27 veranschaulichte Lonchorhynchus-Schädel stellt eine Rekonstruktion dar, die von uns auf Grund einer genügenden Menge gut erhaltener Abdrücke und Fragmente dieses Labyrinthodonten angefertigt war (Arbeiten von WIMAN, 1914, 1916, 1917).

Die WIMAN zur Verfügung gestandenen gesonderten Stücke gewährten ihm die Möglichkeit den Gesamtschädel von *Lonchorhynchus* wiederherzustellen. Es fehlte bloss ein unerheblicher Bezirk an der Schnauzenspitze (der distale Teil der Praemaxillaria). In seinen Rekonstruktionen schliesst WIMAN mutmasslich die Schnauze von *Lonchorhynchus* mit einem Zuspitzen ab. Bei *Platyops*, dessen Schädel den Gesamtumrissen nach mit dem Lonchorhynchus-Schädel grosse Ähnlichkeiten besitzt, waren die Enden des Ober- und Unterkiefers etwas erweitert. Wir pflichten der Ansicht I. A. EFREMOVS bei (1933), der eine analoge Erweiterung an den Kieferenden auch bei *Lonchorhynchus* anerkennt und

Abb. 27. Lonchorhynchus Öbergi. Rekonstruktion nach den von WIMAN veröffentlichten Materialien.

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bewerkstelligen es an unserer Rekonstruktion. Somit weicht unsere Abbildung lediglich durch diese Einzelheit von WIMANS Rekonstruktion ab.

Die drei Zonen des intensiven Wachstums bei *Lonchorhynchus* ordnen sich auf dessen Schädel folgendermassen an. Die erste — relativ schwache Zone, — liegt zwischen dem Foramen parietale und den Orbiten. Sie ist durch das gesteigerte Wachstum der Vorderränder der Parietalia, Supratemporalia, Squamosa, Quadratojugalia und der Hinterränder der Frontalia, Postfrontalia, Postorbitalia und Jugalia bedingt. Das Vorhandensein der Wachstumszone in dem soeben erwähnten Schädelbezirke hatte eine belanglose Verlagerung der Orbiten nach vorne bewirkt. Diese Verlagerung wird sofort augenfällig, falls ein Vergleich zwischen dem Lonchorhynchus — und Platyops-Schädel gezogen wird. Die zweite Zone lagert sich zwischen den Orbiten und den Nasenlöchern und ist auf Kosten der sehr intensiv gewucherten Vorderenden der Frontalia, Praefrontalia, Jugalia und der Hinterenden der Lacrimalia und Nasalia gebildet. Diese Zone des intensiven Wachstums hat die Nasenlöcher beträchtlich weiter nach vorne, als bei *Platyops,* verschoben, Schliesslich lagert sich die dritte Zone zwischen den Nasenlöchern und dem vorderen, etwas erweiterten Schnauzenende. Sie ist durch das aussergewöhnlich intensive nach dem Nasenlöchern zu gerichtete Wachstum lediglich eines Paares der Praemaxillaria bedingt. In diesem Sinne ist die dritte Zone der entsprechenden Zone bei *Platyops* analog, doch ist sie bei *Lonchorhynchus* schärfer ausgeprägt.

Die drei Zonen des intensiven Wachstums haben dem Schädel von *Lonchorhynchus Öbergi* die Form eines langen Keils beigebracht.

Das System der Furchen des Schleimkanals ist bei ihm zur Genüge gut ausgeprägt. Es bestätigt wiederum die These, dass der Verlauf des Schleimkanals bei sämtlichen Stegocephalen vollkommen von der Lokalisierung der Ossifikationszentren derjenigen Schädelknochen abhängt, mit denen der Kanal in Verbindung steht. Auch *Lonchorhynchus Öbergi* stellt in dieser Beziehung, trotz des Vorhandenseins dreier Zonen des intensiven Wachstums, die dessen Schädel in einen sehr langgestreckten Keil umgewandelt hatten, keine Ausnahme dar.

In Anbetracht der von WOODWARD (1908) und WIMAN (1914) beschriebenen Schädelreste ist es anzunehmen, *Aphaneramma rostratum* gehöre, der Zahl und Anordnung der Zonen des intensiven Wachstums zufolge, demselben Typus wie *Lonchorhynchus Öbergi* an.

Gruppe IV.

Wie bereits erwähnt, rechnen wir der vierten Gruppe diejenigen Stegocephalen zu, deren Schädel keinerlei Zonen des intensiven Wachstums besitzen. Beim Ausbleiben dieser Zonen ist die Länge des Stegocephalen-

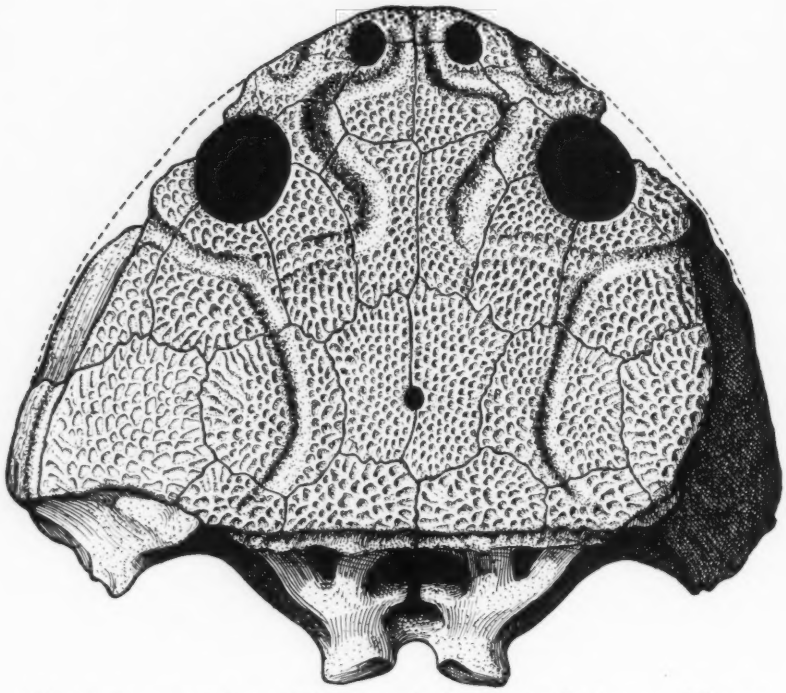

Abb. 28. Batrachosuchus. Abbildung nach der Photoaufnahme von WATSON.

Schädels fast dessen Breite gleich. In dem in Rede stehenden Fall haben wir ausschliesslich Schädel der erwachsenen Tiere im Auge, da den Larven- und Jungformen überhaupt kurze und breite Schädel eigen sind.

Jugendliche *Benthosaurus sushkini* (Abb. 15) und *Archegosaurus Decheni* (BURMEISTER, 1850; v. MEYER, 1856—1858) hatten relativ kurze Schädel, deren Länge die Breite in weitaus geringerem Grade, als bei den erwachsenen Exemplaren derselben Gattungen übertraf. Die Verlängerung des Schädels bei erwachsenen *Benthosaurus* und *Archegosaurus* war durch das Vorhandensein der Zone des intensiven Wachstums in der Präorbitalregion bedingt. Daraus erhellt, dass falls die betreffende Spezies der Stegocephalen keine Zone des intensiven Wachstums besessen hätte, so müsste der Schädel deren Vertreter auch in erwachsenem Zustande die „Larvenform" bewahren. Ein Beispiel eines derartigen Stegocephalen ist der von BROOM (1903) und WATSON (1920) beschriebene *Batrachosuchus browni*. Seine Schädellänge beträgt 250 mm.

Die Deckknochen des Schädels von *Batrachosuchus* (Abb. 28) stellen fast quadratische Gebilde dar, die auf ihrer Gesamtoberfläche mit rundwabiger Skulptur bedeckt sind. Kein einziger Schädelknochen besitzt einen mit langen Kämmen bedeckten Bezirk, was der Zone des intensiven Wachstums eigen

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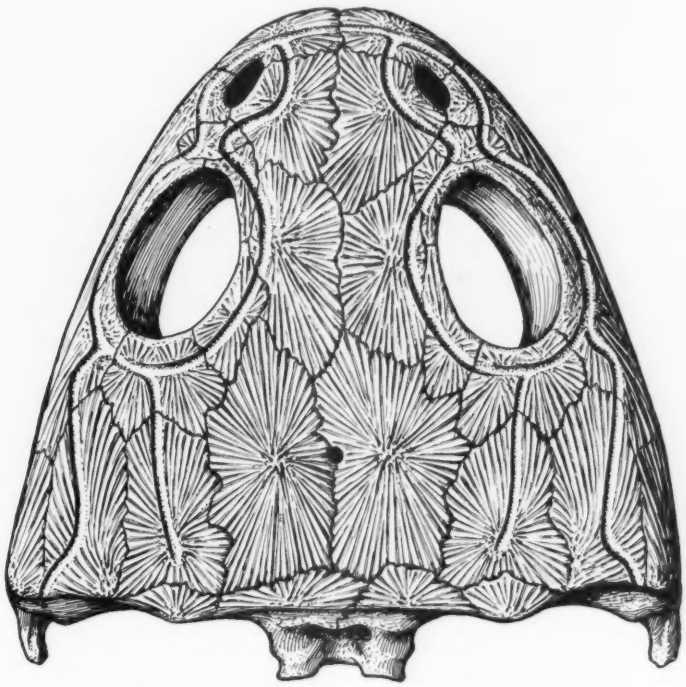

Abb. 29. Dwinosaurus primus AMALITZKY.

ist. Demnach entspricht die Knochenskulptur vollständig der Schädelform. *Batrachosuchus*, der keine Zonen des intensiven Wachstums besass, hat auch im erwachsenen Zustande einen kurzen und breiten Schädel bewahrt, der ihm im Larvenstadium der Entwicklung eigen war.

Die Schleimkanäle von *Batrachosuchus*, in Anbetracht der breiten und tiefen Furchen am Schädel, waren sehr kräftig entwickelt und erstreckten sich auf denjenigen Knochen, an welchem sie gewöhnlich bei sämtlichen Stegocephalen verlaufen.

Ausser *Batrachosuchus* ist der vierten Gruppe eine Reihe von Stegocephalen zuzurechnen, und zwar — *Keraterpeton crassum, Dawsonia polydens, Microbrachis Pelikani* (FRITSCH, 1880, 1881, 1884; Ob. Karbon), *Branchiosaurus amblistomus* (Ob. Karbon und Unt. Perm), *Pelosaurus laticeps* (CREDNER, 1885; Unt. Perm) und der von OWEN (1855) beschriebene Stegocephal (vermutlich aus der Trias) — *Brachyops laticeps*. Es sei hier noch *Dwinosaurus* beigefügt. Doch weist dieser Stegocephal aus dem oberen Perm eine Reihe äusserst interessanter Eigentümlichkeiten auf, infolgedessen wollen wir uns mit ihm etwas eingehender befassen.

Dwinosaurus stellt einen Stegocephalen dar, der anscheinend keine den Amphibien übliche Metamorphose durchgemacht hatte. Darauf weisen die

erhalten gebliebenen Reste der Skelettelemente des Kiemenapparates hin. W. P. AMALITZKY hat drei Dwinosaurus-Spezies in Kürze beschrieben: *D. primus, D. secundus* und *D. tertius*. Die Gesamtlänge des Tieres betrug nach der Ansicht von AMALITZKY 1 Meter oder etwas darüber. Die Schädellänge von *D. primus* mass 175 mm, von *D. secundus* — 220 mm und von *D. tertius* — 180 mm. Die Materialien von AMALITZKY befinden sich zur Zeit im Paläozoologischen Institut der Akademie der Wissenschaften der UdSSR und waren unserer unmittelbaren Erforschung zugänglich.

Vor allen Dingen interessierten uns drei Besonderheiten des *Dwinosaurus:* 1. Vorhandensein der Skelettelemente des Kiemenapparats, 2. Skulptur der Schädelknochen und 3. Verlauf der Furchen des Schleimkanals.

Das Vorhandensein der Reste des Skeletts des Keimenapparats weist unzweifelhaft darauf hin, dass es sich gegebenenfalls um eine Larve sehr grosser Dimensionen handelt. Der Dwinosaurus-Schädel ist kurz, von fast regelmässiger dreikantiger Form, was für die Beibehaltung der primitiven Züge, die in diesem oder jenem Grade sämtlichen Larvenform eigen sind, spricht. Die Knochen von *Dwinosaurus* wuchsen mehr oder minder regelrecht nach allen Seiten hin, ohne die primitiven Schädelumrisse zu modifizieren. Zonen des intensiven Wachstums sind im Schädel nicht vorhanden.

Dwinosaurus blieb sichtbar sein lebenlang eine Larve, infolgedessen tragen sämtliche Dermalknochen seines Schädels an ihrer Oberfläche charakteristische Eigentümlichkeiten einer Larve. Immerhin sticht deren radiale Streifung beträchtlich gegen die Knochenskulptur der üblichen Larven ab. Das Gesamtgepräge der von dem Ossifikationszentrum eines jeglichen Schädelknochens divergierenden radialen Strahlung ist hier beibehalten, doch haben sich diese Strahlen bei *Dwinosaurus primus* (Abb. 29) in hohe und scharfkantige Kämme umgewandelt. Die Knochen gestalteten sich nunmehr statt relativ glatt und leicht gestrichelt mit grobradialer Skulptur bedeckt. Eine rundwabige Skulptur fehlt bei *Dwinosaurus primus* an sämtlichen Schädelknochen.

Bei dem etwas grösseren *Dwinosaurus tertius* ist die Skulptur am Schädel eine andersartige. Abbildung 30 gibt das Bild seines Schädels wieder. Dabei ist die Knochenskulptur auf Grund der Erforschung sowohl des ganzen Schädels dieser Gattung, an dem das Relief der Knochenoberfläche nicht in sämtlichen Bezirken bestehen geblieben war, als auch der einzelnen besser erhaltenen Fragmente, die derselben Spezies angehören, rekonstruiert. Dies gewährte die Möglichkeit das komplette Bild der Skulptur am Schädel wiederherzustellen.

Die Kämme sind an der Oberfläche der Dermalknochen des Schädels von *Dwinosaurus tertius* kräftiger als bei *Dwinosaurus primus* ausgeprägt. Sie streben divergierend von den Ossifikationszentren radial und stellen dabei

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Abb. 30. Dwinosaurus tertius AMALITZKY.

ein ganz eigenartiges Bild dar. Die rundwabige Skulptur fehlt bei *Dwinosaurus tertius* selbst im Bereiche der Ossifikationszentren (S. Abb. 10 A).

Bei *Dwinosaurus secundus* ist die Knochenskulptur sehr schlecht erhalten geblieben, doch zeugen einige Überreste derselben davon, dass sie ihrem Charakter nach grundsätzlich durch nichts von der Skulptur des *Dwinosaurus tertius* abweicht.

Sämtliche von W. P. AMALITZKY als gesonderte Gattungen beschriebenen Dwinosauren stellen aller Wahrscheinlichkeit nach lediglich drei Exemplare verschiedenen Alters, doch ein und derselben Spezies dar. Dieser Ansicht pflichtet auch I. A. EFREMOV bei (1932).

Von grossem Interesse ist die Mikrostruktur der Deckknochen des *Dwinosaurus*. Auf Abb. 31 ist das Bild des Querschliffs durch einen von den Kämmen an dem Supratemporale von *Dwinosaurus tertius* wiedergegeben. Diese Kämme sind im Grunde keineswegs denjenigen von *Benthosaurus* homolog, da sie, sich radial vom Ossifikationszentrum bis zu den Knochenrändern lagernd, auf ihrer ganzen Ausdehnung nirgends eine rundliche Wabe begrenzen. Gleichwie die Kämme von *Benthosaurus* bestehen sie aus einer grossen Anzahl gebogener Platten der Knochensubstanz, ermangeln jedoch total desjenigen Netzes der feinen Kanälchen, das für den erwachsenen

Benthosaurus so kennzeichnend ist. Zu Grunde eines jeden Kammes lässt sich ein Zentralkanal (b) ermitteln, welcher von denjenigen Knochenplatten überschichtet wird, die den Kamm selbst ausbilden. Der Knochen von *Dwinosaurus* trägt Spuren eines beträchtlichen Umbaus. In der Mitte des Knochens sind grosse Höhlen (a), die kraft des Resorptionsvorgangs entstanden sind, sichtbar. In den Kämmen selbst lassen sich nicht selten neugebildete Kanäle mit ihrem eigenen „Haverschen System" (c) nachweisen. Trotz des beträchtlichen Umbaus ist der Knochen von *Dwinosaurus*, der die Kiemen bewahrt hatte, als weniger spezialisiert im Vergleich zum Knochen des lungenatmenden *Benthosaurus* anzuerkennen. Ersterer stellt offenbar lediglich einen stark hypertrophierten Larvenknochen dar und entspricht der sog. „Basallamelle" der Deckknochen des erwachsenen *Benthosaurus*.

Das Vorhandensein des Kiemenapparats, das Erhaltenbleiben der Larvenform des Schädels und des Larvencharakters im Knochenbau mit nachfolgender Verstärkung sämtlicher Larveneigentümlichkeiten der Schädelskulptur spricht unzweifelhaft dafür, dass *Dwinosaurus* etwas in der Art des „Permischen Axolotl" darstellt. Es wäre schwerlich sich dahin zu äussern, ob er im Laufe seines Lebens die Lungenatmung erwarb, die grobradiale Skulptur der Larvenknochen seines Schädels durch die rundwabige der erwachsenen Formen ersetzte, oder ständig im Stadium „der Larve" verblieb, deren Länge von etwas über ein Meter war. Fand die Metamorphose bei *Dwinosaurus* statt, so musste dessen Schädel nach dem Ersatz der Kiemen durch die Lungen anscheinend Formen und Skulptur erhalten, die denjenigen bei *Batrachosuchus* sehr nahe standen.

Es ist anzunehmen, die Behinderung der Metamorphose wäre keine ausschliessliche Eigentümlichkeit des *Dwinosaurus*. Die von Moodie (1909) beschriebenen *Stegops divaricata* und *Tuditanus tabulatus* blieben wahrscheinlich ebenso lange im Larvenstadium. Diese beiden Gattungen hatten an den Schädelknochen eine radiale Skulptur. (Über *Stegops divaricata* s. die Arbeit von M. Steen, 1930.) Doch wich letztere von der üblichen radialen Beschaffenheit der Larvenformen wesentlich ab. Die Kämme sind bei *Stegops* und *Tuditanus* ungleich kräftiger ausgeprägt. Dem Charakter ihrer Skulptur zufolge erinnern diese Stegocephalen sehr an *Dwinosaurus*. Es liegt die Möglichkeit vor, dass beide (zumal *Stegops divaricata*) eine ebenso anhaltende Behinderung der Metamorphose besassen, wie es bei *Dwinosaurus* der Fall war. Die Gesamtumrisse des Schädels, die Anordnung der Augenlöcher und des Parietallochs bei *Tuditanus tabulatus* erinnern dermassen an *Dwinosaurus*, dass bereits W. P. Amalitzky auf die Ähnlichkeit dieser Spezies hingewiesen hat.

Von nicht geringerem Interesse sind die Furchen an den Knochen des Dwinosaurus-Schädels, als Spuren dessen Schleimkanäle.

Die Furchen des Scheimkanals bei *Dwinosaurus* verlaufen wie bei sämt-

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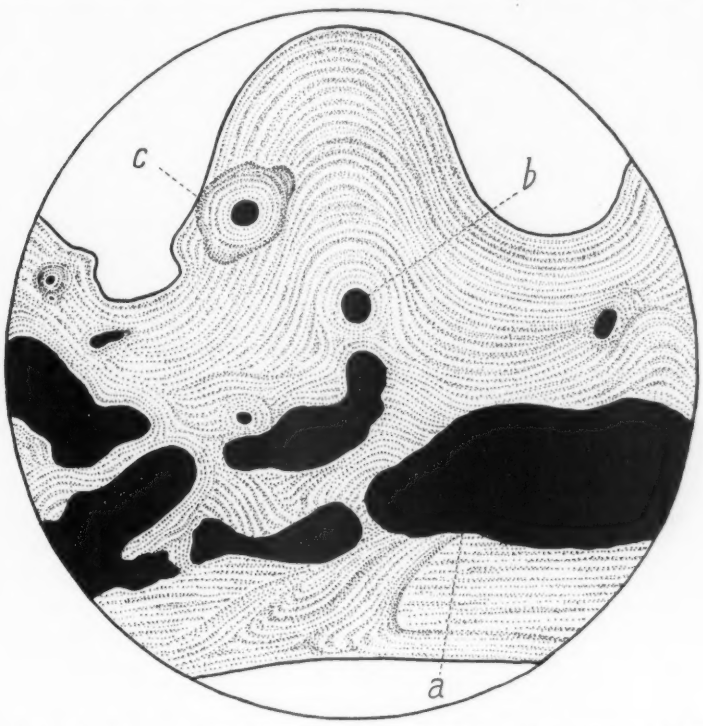

Abb. 31. Querschliff durch den Kamm des Deckknochen von Dwinosaurus (Vergrössert um 30mal).

lichen Stegocephalen von einem Ossifikationszentrum zum anderen und durchziehen dieselben Knochen, wie bei einer beliebigen der besprochenen Gattungen. Doch ist bei *Dwinosaurus* eine sehr interessante Eigentümlichkeit vorhanden. Wie bereits erwähnt, überschneidet bei einigen Stegocephalen aus dem Karbon, gleichwie bei *Ichthyostegidae* und *Osteolepis macrolepidotus* aus dem Devon der Canalis jugalis das Ossifikationszentrum des Squamosum, was bei erwachsenen Stegocephalen des Perm und der Trias nicht statthat. Wir halten die Anwesenheit eines derartigen Kanals bei den Stegocephalen für ein Merkmal der Primitivität, welches sie mit den *Crossopterygii* verbindet. Der Canalis jugalis ist bei *Dwinosaurus* gut ausgeprägt und, was für uns besonders von Belang ist, durchzieht er, einen Bogen bildend, das Squamosum (Abb. 30). Diese Eigentümlichkeit ist unseres Erachtens von grossem theoretischen Interesse. Sie stellt zweifelsohne eines von dem Merkmalen der Primitivität in der Organisation des *Dwinosaurus* dar, da sie ihn mit *Ichthyostegidae* und *Osteolepis* näher bringt. Es liegt die Möglichkeit vor, dass das Vorhandensein dieser Furche mit dem Erhaltenbleiben im Larvenstadium einiger den Urformen eigenen Besonderheiten im Zusammenhang steht.

Die Mehrzahl der Stegocephalen lässt sich der Anordnung der Zone (oder Zonen) des intensiven Wachstums im Schädel zufolge ohne Schwierigkeit diesem oder jenen Typus der betreffenden Gruppe zuzurechnen. Eine Ausnahme bildet eine von den spätesten Gattungen der Labyrinthodonten — *Plagiosaurus* (obere Trias). Die Schädel von *Plagiosaurus granulosus* (Abb. 32 C) und *Plagiosaurus pulcherrimus* (Fraas, 1913) besitzen eine ganz eigenartige Form. Der Anordnung der Wachstumszonen gemäss darf weder die eine noch die andere Spezies von *Plagiosaurus* einem von unseren Typen zugerechnet werden. Dessen Wachstumszonen lagern sich den Seiten der Orbiten an; infolgedessen wurde der Schädel bei relativ geringer Länge sehr breit. Die Schädellänge von *P. granulosus* beträgt 200 mm, die Breite 500 mm; bei *P. pulcherrimus* bzw. 125 und 300 mm. Bei diesen Formen erweisen sich die Wachstumszonen als paarig und durch sehr grosse Orbiten getrennt. *Plagiosaurus* ist unzweifelhaft eine hochspezialisierte Gattung der späteren Labyrinthodonten, doch ist seine Spezialisierung derjenigen einer derartigen Gattung wie *Lonchorhynchus Öbergi* diametral entgegengesetzt.

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IV.

Im Jahre 1933 hat I. A. Efremov erstmalig verzeichnet, dass das Parietalloch in sämtlichen Modifikationen des Stegocephalen-Schädels sich als ein unbeweglicher Punkt darbietet. Unsere Untersuchungen bestätigen diesen Satz in vollem Masse. Bei der Erforschung dieser Frage stellte es sich heraus, dass, abgesehen von Zahl und Typus der Anordnung der Zonen des intensiven Wachstums und folglich der Gesamtform des Schädels, das Foramen parietale bei sämtlichen Stegocephalen stets auf denjenigen Punkt des Parasphenoideum projiziert, wo von selbigem der Processus cultriformis nach vorne abgeht. Auf Abb. 32 sind die Schädelbasis von *Platyops watsoni* (A), *Diplocaulus magnicornis* (B), *Plagiosaurus granulosus* (C), *Batrachosuchus browni* (D) und *Diceratosaurus punctolineatus* (E) dargestellt. An sämtlichen Schädeln ist die Projektion des Parietallochs auf die Basis des Processus cultriformis durch einen kleinen Kreis bezeichnet. Diese Projektion bleibt in sämtlichen Fällen unverändert, welche immer die Schädelform der betreffenden Spezies der Stegocephalen auch sein mag.

Bei starker Verlängerung des Schädels (z. B. bei *Platyops watsoni* — Abb. 32 A, — und noch mehr bei *Lonchorhynchus Öbergi* — Abb. 33 A) streckt sich der Processus cultriformis parasphenoidei kräftig in die Länge und wird sehr schmal.

Die Rami anteriores der Pterygoiden nehmen am Vorgange der Schädelverlängerung keinen grossen Anteil. Die Fossae temporales (F. t., Abb. 32 und 33), die medial an die Rami anteriores der Pterygoiden grenzen, verändern

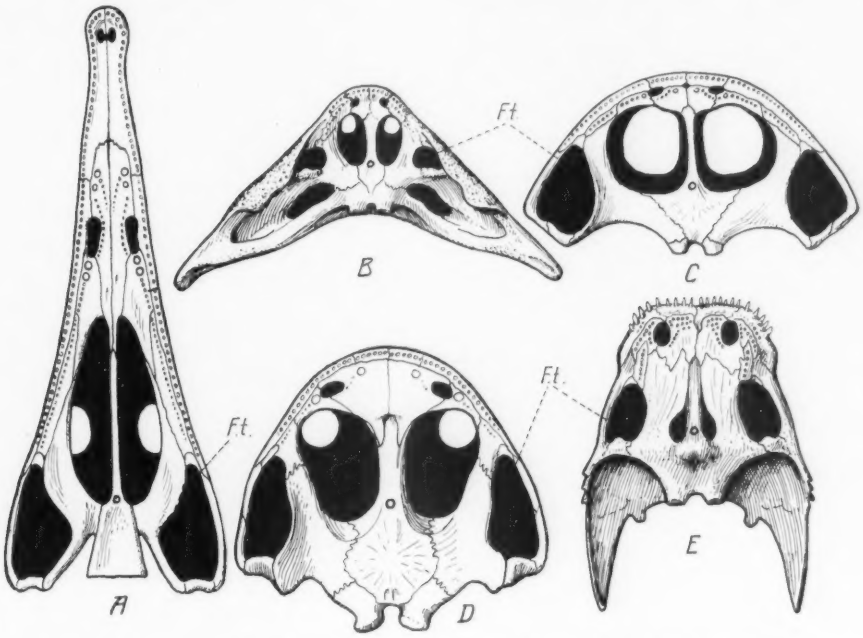

Abb. 32. Basis cranii. *A* Platyops watsoni (Rekonstruktion), *B* Diplocaulus magnicornis, *C* Plagiosaurus granulosus, *D* Batrachosuchus, *E* Diceratosaurus punctolineatus.

sich ihrer Form und relativen Grösse nach bei der Gesamtverlängerung des Schädels nur wenig. Dies ist dadurch zu erklären, dass die Schläfengruben als Austrittsstelle der Gruppe der Musculi masticatores, die dem Unterkiefer anhaften, dienen. Der Komplex der die Kiefer zusammenpressenden Muskeln lagert sich selbstverständlich in sämtlichen Fällen nach vorne zum Kiefergelenke, welches durch das Quadratum (am Schädel) und das Articulare (am Unterkiefer) gebildet ist. Diese Muskeln wären jedweder Bedeutung verlustig geworden, hätten sie sich bei einer derartigen Spezies der Labyrinthodonten, wie *Lonchorhynchus Öbergi*, zugleich mit der kräftigen Verlängerung des Gesamtschädels ebenfalls nach vorne verschoben. In diesem Falle hätte das Tier allerdings sehr an Stärke des Zusammenpressens seiner Kiefer gewonnen, wäre jedoch nicht imstande bei kurzen Kaumuskeln seine langen und schmalen Kiefer hinreichend weit zu eröffnen. Derartige Keilformen des Schädels, wie bei *Lonchorhynchus* und *Platyops* waren wahrscheinlich den sehr beweglichen und gut schwimmenden Gattungen der Labyrinthodonten eigen, die zum Haschen der Beute vermöge der langen und schmalen, mit zahlreichen Zähnen ausgestatteten Kiefer angepasst waren. Dabei erlitt das Tier infolge der Anordnung der Kaumuskeln in der hinteren Schädelpartie allerdings einen Verlust an der Stärke des Zusammenpressens, entschädigte sich jedoch beträchtlich durch die Beweg-

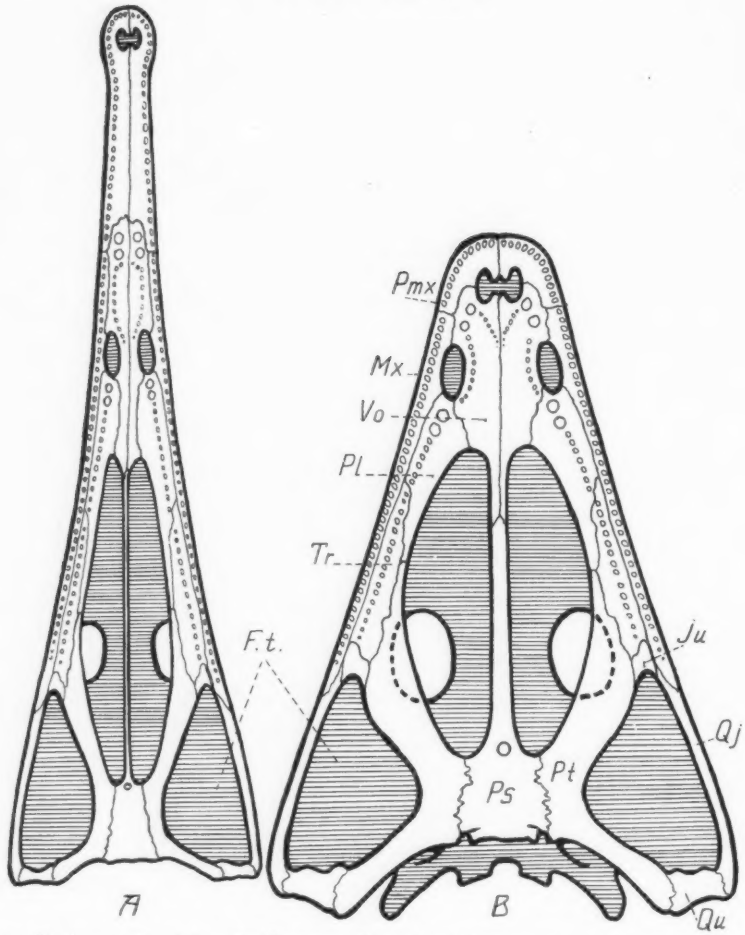

Abb. 33. Basis cranii. *A* Lonchorhynchus Öbergi (Rekonstruktion des Autors nach den Materialien von WIMAN), *B* Benthosaurus sushkini. *Pmx.* Praemaxillare, *Mx.* Maxillare, *Vo.* Vomer, *Pl.* Palatinum, *Tr.* Transversum, *Ju.* Jugale, *Qj.* Quadratojugale, *Pt.* Pterygoideum, *Ps.* Parasphenoideum, *F. t.* Fossa temporalis.

lichkeit des Kieferapparats. Im Gegenteil verfügten bei kurzköpfigen Formen der Stegocephalen (*Diplocaulus, Batrachosuchus* und zumal *Plagiosaurus*) die Kiefer unzweifelhaft über einen relativ geringeren Schwung der Bewegung, waren indessen kräftiger.

Demnach erweisen sich beide Fossae temporales im Sinne ihrer Lage im Schädel mit der Articulatio mandibularis verbunden. Und diese Verbindung bleibt ungestört, welche Form der Schädel auch immer erhalten mag. Bei den Stegocephalen mit langen Schädeln (*Benthosaurus, Trematosaurus, Lonchorhynchus*) verlängern sich die Schläfengruben, in der hinteren Schädelpartie verbleibend, fast nicht und ändern nur wenig ihre Umrisse. Die Ver-

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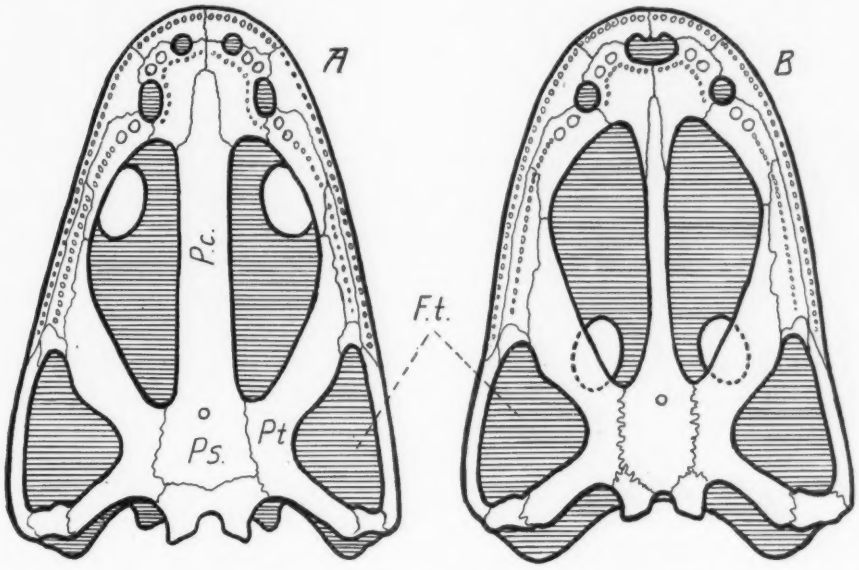

Abb. 34. Basis cranii. *A* Metoposaurus diagnosticus, *B* Cyclotosaurus. *Pc.* Processus cultriformis parasphenoidei, *Ps.* Parasphenoideum, *Pt.* Pterygoideum, *F. t.* Fossa temporalis.

längerung des Schädels vollzieht sich in diesen Fällen auf Kosten des intensiven Wachstums derjenigen Knochen der Basis, die nach vorne zu den Fossae temporales gelegen sind (Transversum, Palatinum, Vomer, Praemaxillare — Abb. 33). In der hinteren Schädelpartie dagegen kommt ein unveränderlicher Komplex der Knochen zustande, die funktionell miteinander verbunden sind: Quadratojugale, Quadratum, Pterygoideum, Jugale, welche die Fossae temporales begrenzen und das mit den Pterygoidea verankerte Parasphenoideum.

Was die Augen- und Nasenlöcher anbelangt, so steht ihre Lage im Schädel mit der Zahl und dem Typus der Anordnung der Zonen des intensiven Wachstums im Zusammenhang. Dies ist besonders bei dem Vergleiche der Metoposaurus- und Cyclotosaurus-Schädel augenfällig. Wie bekannt gehören diese beiden Labyrinthodonten einem und demselben Zeitraum (der oberen Trias) an und ihre Schädel stehen den Gesamtumrissen und den fast gleichen Dimensionen zufolge einander nahe. Der Lage der Zone des intensiven Wachstums nach gehören sie jedoch verschiedenen Typen der ersten Gruppe an. Die Zone des intensiven Wachstums liegt bei *Metoposaurus* zwischen dem Foramen parietale und den Orbiten (2. Typus), bei *Cyclotosaurus* — zwischen den Nasen- und Augenlöchern (3. Typus). Die Zone des intensiven Wachstums hat bei *Metoposaurus* eine Verlagerung nach vorne der Orbiten und Nasenlöcher, bei *Cyclotosaurus* lediglich der Nasenlöcher

hervorgerufen; die Orbiten sind bei ihm in der hinteren Schädelpartie geblieben. Die Bilder der Schädelbasis dagegen sind in diesen beiden Fällen (Abb. 34) im wesentlichen identisch geblieben. Die Differenzen bestehen bloss darin, dass der Processus cultriformis bei *Metoposaurus* ungleich stärker als der betreffende Fortsatz bei *Cyclotosaurus* ist. Somit modifiziert in einigen Fällen die verschiedenartige Lokalisation der Zonen des intensiven Wachstums, eine Verlagerung der Augen- und Nasenlöcher bewirkend, die Gesamtumrisse des Schädels und den Aufbau dessen Basis nicht.

Sogar Schädel der Stegocephalen, die der Lage der Wachstumszonen nach nicht lediglich verschiedenen Typen, sondern auch verschiedenen Gruppen angehören, können einen fast identischen Bau der Basis cranii besitzen. Beispielsweise erwähnen wir *Benthosaurus* (I. Gruppe, 3. Typus) und *Trematosaurus* (II. Gruppe, 2. Typus). Auch hier hat die Differenz der Anzahl der Wachstumszonen lediglich Verschiedenheit in bezug auf die Lage der Orbiten bewirkt; die Schädelbasis lassen sich bei diesen Labyrinthodonten nur wenig von einander unterscheiden.

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Daraus ergibt sich die Folgerung, dass die Anzahl der Zonen des intensiven Wachstums und der Typus ihrer Anordnung in höherem Grade den Bau der dorsalen Schädelpartie, als die Schädelbasis beeinflusst. Die nach vorne zu den Fossae temporales liegenden Knochen der Schädelbasis verlängern sich bei Stegocephalen mit keilförmigem Schädel gleichmässig, der Gesamtverlängerung des Schädels parallel. In der Schädelbasis lassen sich keine isolierten Wachstumszonen nachweisen; die Basis cranii wächst, sich lediglich dem Gesamtwachstum des Schädels unterziehend und zwar bloss in dem den Fossae temporales vorliegenden Teile. Der mit der Kaumuskulatur und dem Gehirn verbundene Hinterteil der Basis cranii stellt ein zähes, wenig variables anatomisches Gebilde dar.

Der Unterkiefer bei sämtlichen Stegocephalen verhält sich im Grunde zu den Zonen des intensiven Wachstums, ebenso wie die Schädelbasis. Im ersteren lassen sich zwei Abschnitte unterscheiden: der erste (hintere) standhafte und der zweite (vordere) sehr variable Abschnitt. Die Kaumuskulatur, an die Knochen, die den hinteren Abschnitt der Mandibula bilden, haftend, gestaltet ihn zu einem ebenso stabilen Gebilde, wie die Fossa temporalis. In dem hinteren Abschnitte des Kiefers vereinigt sich das Articulare, welches eine Gelenkgrube besitzt, zu einem Gelenke mit dem Quadratum; das Supraangulare und Angulare bilden mitsamt dem Praearticulare (an der Innenseite des Kiefers) eine tiefe Grube, in welche die an dem Kiefer haftenden Kaumuskeln geraten. Demnach stellt dieser Knochenkomplex eine Applikationsstelle der Kräfte sämtlicher die Kiefer zusammenpressenden Muskeln dar. Dabei lagert sich das Ossifikationszentrum des Angulare, welches eine fächerartige Skulptur an seiner äusseren Oberfläche besitzt, genau der Mitte der Fossa temporalis gegenüber. Derartige nach vorne zu liegenden Knochen,

wie Spleniale, Postspleniale, Dentale und mehrere Knochen an der Innenseite dienen zur Verlängerung des Kiefers bloss als eines Hebels. Die Zunahme des vorderen Abschnitts des Unterkiefers an Länge vollzieht sich in sämtlichen Fällen auf Kosten des intensiven Wachstums dieser Knochen, die mit der Kaumuskulatur in keiner direkten Verbindung stehen. Der gesamte hintere Knochenkomplex des Unterkiefers bleibt stets unverändert, welche Länge der Schädel auch immer erreicher mag. Dieser Komplex verändert sich lediglich in Zusammenhang mit den Modifikationen in der Stärke der Musculi masticatores und diese Modifikationen gehen denjenigen der Fossa temporalis parallel vor sich. Daraus erhellt, aus welchem Grunde die Unterkiefer verschiedener Spezies der Labyrinthodonten so wenig von einander

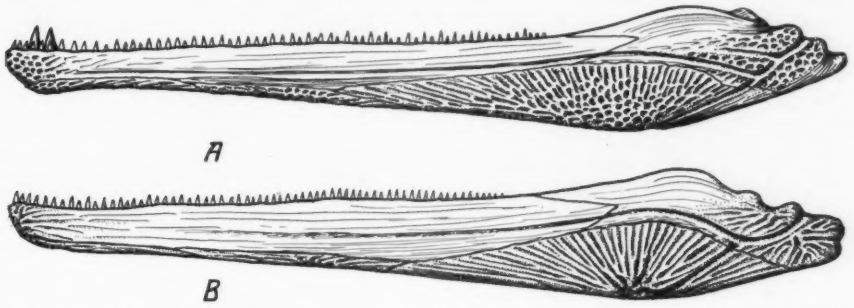

Abb. 35. *A* Mandibula von Benthosaurus sushkini, *B* Mandibula von Dwinosaurus tertius Amalitzky.

abweichen. Verschiedenheiten sind bloss in der Länge ihres Vorderteils und in einigen Varianten des Massivs des Hinterteils vorhanden. Ersteres ist durch die Gesamtlänge des Schädels, letzteres durch die Stärke der Kaumuskulatur bedingt. Der Unterkiefer der Labyrinthodonten kommt bloss zwei Ansprüchen nach: er muss einen relativ unveränderlichen und stabilen Knochenkomplex als Ansatzstelle der Kaumuskeln in seinem Hinterteile gewähren und sich im Vorderteile dermassen verlängern, um der Gesamtlänge des Schädels conform zu sein. Dabei beeinflusst das Vorhandensein dieser oder jenen Anzahl der Zonen des intensiven Wachstums im Schädel selbst, sowie der Typus der Anordnung dieser Zonen die morphologischen Eigentümlichkeiten des Unterkiefers nie und auf keinerlei Weise. Infolgedessen, lediglich über ein Unterkiefer verfügend, ist es unmöglich sich dahin zu äussern, welcher Gruppe und welchem Typus, der Anzahl und Lage der Zonen des intensiven Wachstums zufolge, der Schädel der betreffenden Gattung der Stegocephalen zuzurechnen wäre und in welchen Bezirken der Schädeldecke die Augen- und Nasenlöcher gelegen waren.

Auf Abb. 35 sind zwei Unterkiefer dargestellt. Der eine von ihnen (A) gehört einem erwachsenen *Benthosaurus* an (mit einer Zone des intensiven Wachstums und keilförmigem Schädel); der andere (B) einem *Dwino-*

saurus, der einen kurzen Schädel ohne Wachstumszonen besitzt. Beide Kiefer weichen ihrer Form nach wenig voneinander ab. Der längste Knochen des Unterkiefers ist das Dentale. Seine Länge ist derjenigen des gesamten bezahnten Teils des Kiefers gleich. Diesem Knochen gegenüber lagern sich im Schädel zwei Knochen: Praemaxillare und Maxillare. Von ihnen weist das Maxillare das kräftigste Wachstum auf. Dieser Knochen wächst gleichwie das Dentale unabhängig von der Anzahl und dem Typus der Anordnung der Wachstumszonen im Schädel, obgleich er einen von den Knochen des Gesichtsschädels darstellt. Die anatomische Struktur des Stegocephalen-Schädels stellt dem Maxillare im wesentlichen dieselben Postulate, wie dem Dentale: dieser Knochen muss mitsamt dem Praemaxillare von einer Länge sein, die der Schädellänge von der Fossa temporalis bis zum vorderen Schnauzenrande conform wäre. Demnach besitzt das Maxillare seine eigene konstante Zone des intensiven Wachstums, die ihr stets den obigen Anspruchen nachzukommen gestattet. Infolge dieser Besonderheit des Maxillare haben wir bei der Beschreibung der verschiedenen Typen der Stegocephalen-Schädel in der Mehrzahl der Fälle ersteres in den Komplex der die eine oder die andere Zone des intensiven Wachstums bildenden Knochen nicht eingeschlossen.

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Auf Grund des bereits analysierten Materials können wir mit Sicherheit behaupten, die Zonen des intensiven Wachstums wären wenn nicht der einzige, immerhin der wichtigste Faktor, der die Veränderung der Schädelform der Stegocephalen sicherstellt. Was sodann die Augen- und Nasenlöcher anbelangt, so hängt ihre Lage im Schädel vollkommen von der Anzahl und der Lokalisation dieser Zonen ab.

Verschiedenen Stegocephalen-Spezies sind, wie bereits besprochen, verschiedene Typen der Anordnung und verschiedene Mengen der Zonen eigen. Letztere geben sich nicht lediglich bei phylogenetischen Veränderungen, sondern auch im Vorgange der individuellen Entwicklung der Stegocephalen kund, deren Schädelform nach dem der betreffenden Spezies eigenen Typus modifizierend. Immerhin ist die Zone des intensiven Wachstums nicht als Ursache der Veränderungen des Schädels zu betrachten. Die Wachstumszone ist unseres Erachtens lediglich ein Mittel, an dessen Hand der Stegocephalen-Schädel diese oder jene Form im Anpassungsvorgange des Tieres zu seinen Existenzbedingungen gewinnt.

Verschiedene Kombinationen in der Lage und Varianten in der Anzahl der Zonen gewährten den Stegocephalen die Möglichkeit mannigfaltigste Schädelformen zu acquirieren, aus der primitiven Grundform hervorgehend. Diese primitive Schädelform war der Zonen des intensiven Wachstums verlustig. Abgesehen von der primitiven postpinealen Zone (1. Typus der I. Gruppe), stellen alle übrigen Zonen unzweifelhaft ein Merkmal der Spezialisierung der Stegocephalen dar. Von Interesse ist, dass der Grad dieser Spezialisierung, der sich im Zuwachs der Zonen äussert, in Anbetracht der heutzutage vor-

handenen Daten, mit der Entwicklung der Stegocephalia im Laufe eines ungeheuren Zeitraums von dem Karbon bis einschliesslich der Trias immer mehr und mehr zunahm. So besitzen die Stegocephalen aus dem Karbon entweder überhaupt keine Zonen des intensiven Wachstums in ihrem Schädel (*Dawsonia, Microbrachis, Branchiosaurus*) oder sind sie unserer Klassifikation zufolge den primitiven Typen zuzurechnen (*Diceratosaurus, Batrachiderpeton*).

In der Perm kommen bereits zur genüge hochspezialisierte Gattungen mit einer oder gar zwei Zonen des intensiven Wachstums zum Vorschein (*Archegosaurus, Platyops*).

Ihr höchstes Aufblühen hatte die Spezialisierung in der Trias erreicht. Dazumal besassen fast sämtliche uns bekannten Labyrinthodonten Zonen des intensiven Wachstums (*Capitosaurus, Benthosaurus, Mastodonsaurus, Metoposaurus, Anaschisma, Cyclotosaurus* — eine Zone des intensiven Wachstums, *Trematosaurus* und *Tertrema* — zwei). Der Trias gehören auch diejenigen — zwei Gattungen an, die den höchsten Grad der Spezialisierung erreicht hatten, und zwar — *Lonchorhynchus* und *Aphaneramma* mit drei Zonen des intensiven Wachstums. Hier sei noch eine eigenartige Form — *Plagiosaurus* hinzugefügt, bei welcher der Typus der Anordnung der Wachstumszonen sich für die Stegocephalen als vollkommen ungewöhnlich gestaltet. Doch kommen in der Trias ausser diesen hochspezialisierten Formen auch Labyrinthodonten mit nicht scharf ausgeprägten Wachstumszonen (z. B. *Lycrocephalus euri* und *Peltostega Erici*) und mit komplettem Fehlen der letzteren vor (*Brachyops, Batrachosuchus*). Allerdings sind heutzutage derartige primitiven Formen in jeder von den zwei vorhergehenden Perioden in weitaus grösserer Anzahl bekannt. Demnach berechtigt uns das gegenwärtige paläontologische Material die Schlussfolgerung zu ziehen, dass im Evolutionsvorgange der Stegocephalen im Laufe des Karbon, des Perm und der Trias die Menge der spezialisierten Gattungen mit dem Sinken der Zahl der primitiven Formen allmählich zunahm. Diese primitiven kurzköpfigen Formen, die immerhin in dieser oder jener Anzahl der Spezies in jeder der drei Perioden bestehen blieben, dienten sichtbar als Ausgangsmaterial für die Entwickling verschiedener neuer Typen der Spezialisierung, da welche Schädelform der in Rede stehende Labyrinthodont auch haben mochte, er als Nachkomme der kurzköpfigen Gattung zu betrachten wäre.

Als Beleg für diesen Satz dient folgende interessante Erscheinung.

Gewöhnlich lassen sich am Schädel eines jeden Labyrinthodonten, falls er nicht sehr alt ist und die supplementäre Differenzierung der Skulptur sich noch nicht über das Gebiet der radialen Kämme seiner Deckknochen erstreckt hat, die Zonen des intensiven Wachstums gegen die zentralen Zonen ohne Schwierigkeit abgrenzen.

Die Zonen des intensiven Wachstums sind unzweifelhaft ein Ergebnis der Spezialisierung des Stegocephalen und, falls wir erstere von jedem Knochen seines Schädels beseitigen, so erweist es sich, dass wir auf diese Weise auch das Merkmal der Spezialisierung der betreffenden Spezies „eliminieren". Auf Abb. 36 (A) ist der Schädel von *Metoposaurus diagnosticus* (s. Abb. 22) veranschaulicht, auf welchem lediglich rundwabige Bezirke der Zentralzonen dargestellt sind. Die Skulptur der Zonen des intensiven Wachstums ist nicht wiedergegeben, doch sind die Richtungen des intensiven Wachstums der einzelnen Knochen mit Pfeilen bezeichnet. „Verschieben" wir nun sämtliche zentralen Zonen des Metoposaurus-Schädel auf solche Weise, dass ihre Ränder allenthalben knapp einander anliegen, so erzielen wir ein Schädeldach des Stegocephalen, das lediglich aus zentralen Zonen zusammengesetzt ist (Abb. 36, B).

Der auf solche Weise gebaute Schädel erweist sich als kurz und breit. Seinen Gesamtumrissen nach steht er den Schädeln von *Dwinosaurus* (Abb. 29 und 30), *Branchiosaurus, Pelosaurus* und anderer Gattungen, die der Zonen des intensiven Wachstums entbehren, sehr nahe.

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Der auf Abb. 36 (B) dargestellte Schädel ist für die Larvenform des Metoposaurus allerdings sehr gross. Doch lässt er sich ohne Störung der Gesamtumrisse bis auf eine beliebige Grösse verkleinern, da die Zentralzonen, aus welchen er zusammengesetzt ist, gleichmässig nach allen Seiten wachsen und die proportionelle Verringerung ihrer Areale das von uns erzielte Bild allerdings nicht verändern, sondern den gesamten Schädel proportionell verkleinern wird. Bei einer derartigen Verringerung und bei der gleichzeitigen Eliminierung der Wabenskulptur von der Knochenoberfläche werden wir den Schädel einer Metoposaurus-Larve, der noch der Zonen des intensiven Wachstums ermangelte, erzielen (Abb. 36 C).

Dieses graphische Verfahren, bei dessen Anwendung auf Schädel einer beliebigen Spezies der Labyrinthodonten selbst eines solchen wie *Lonchorhynchus Öbergi,* ergibt stets ein und dasselbe Resultat. Somit darf man mit Sicherheit behaupten, dass die zusammengeschobenen Areale der zentralen Schädelzonen eines beliebigen Labyrinthodonten eine und dieselbe Schädelform ergeben. Woraus zu folgern, dass sämtliche verschiedenartigen Spezies der Stegocephalen einer gemeinsamen Form entstammen, die der Zonen des intensiven Wachstums ermangelte und einen kurzen Schädel und relativ grosse Orbiten besass. Diese Schädelform, inwiefern es uns den bislang wenig zahlreichen Funden zufolge bekannt ist, war in diesem oder jenen Grade den langköpfigen Stegocephalen im Larvenstadium deren Entwicklung eigen (Archegosaurus Decheni, H. von Meyer).

Es ist anzunehmen, dass ihrem Schädelbau nach die Urform dem *Pelosaurus* oder *Branchiosaurus* sehr nahe stand. Immerhin wären *Dolichopareias disjectes* (A, Abb. 24), *Diceratosaurus punctolineatus* (Abb. 19), *Batrachi-*

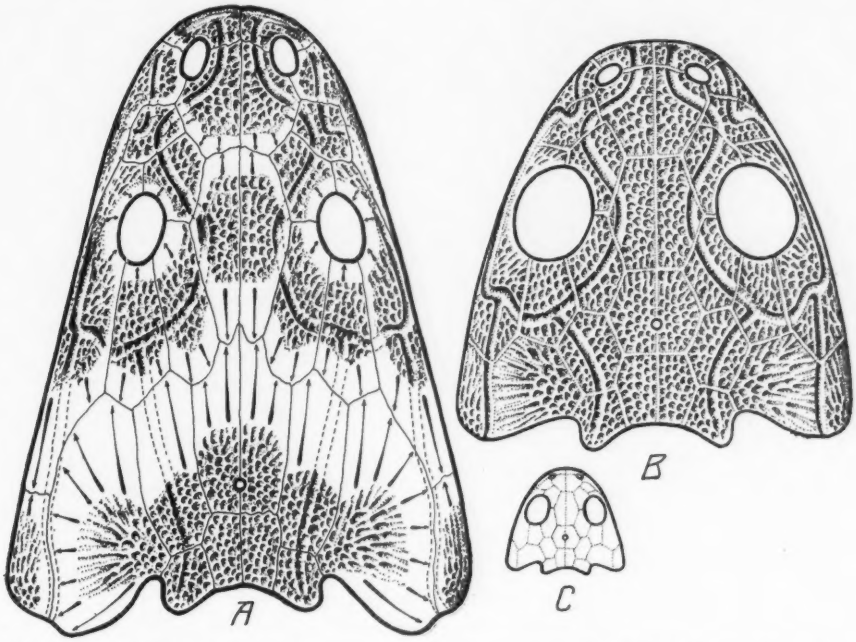

Abb. 36. *A* Schädel von Metoposaurus diagnosticus mit nicht abgebildeten Zonen des intensiven Wachstums, *B, C* Schädel, die lediglich aus den zentralen Zonen der Deckknochen von Metoposaurus zusammengesetzt sind.

derpeton lineatum (Abb. 20) und *Diplocaulus* (Abb. 21), obschon sie sich auf die primitive Form C (Abb. 36) zurückführen lassen, kaum als deren Nachkommen zu betrachten, da die in der postpinealen Partie deren Schädel gelagerte Zone des intensiven Wachstums ein derartiges Merkmal darstellt, welches eher von dem Vorhandensein eines genetischen Zusammenhangs dieser Gattungen mit den Vorfahren des Typus Crossopterygii zeugt. Überdies entspringt die Form C selbst anscheinend aus demselben gemeinsamen Stamm. Doch hat bei ersterer im Evolutionsvorgange bereits eine Reduktion der Dermalknochen der Hinterhauptsgegend des Schädels stattgefunden, infolgedessen kann sie als Ausgangsform für *Diceratosaurus, Batrachiderpeton* und *Diplocaulus* selbstredend nicht dienen.

Was den Typus *Metoposaurus* und *Benthosaurus* anbelangt, so ergibt die Ausbildung der Zonen des intensiven Wachstums bei der Form C in einem Falle zwischen dem Parietalloch und den Orbiten, im anderen zwischen den Orbiten und den Nasenlöchern ohne Schweierigkeit diese beiden Gattungen. Gleichfalls wird das Auftreten zweier Zonen, die in verschiedenen Stellen des Schädels gelagert sind, die Ausbildung der Schädel von *Trematosaurus* und *Platyops* zur Folge haben. Die Höchstzahl der Zonen des intensiven Wachstums (drei) wandelt den kurzen und breiten Schädel der Form

C in einen keilförmigen und oblongen Schädel des Typus von *Lonchorhynchus* um.

Theoretisch wäre das Bestehen eines Labyrinthodonten-Schädels mit vier Zonen des intensiven Wachstums plausibel. Es müsste dazu noch eine Zone in der postpinealen Partie des Lonchorhynchus-Schädels beigefügt werden. Doch wäre dies kaum möglich, da in einem derartigen Schädel eine Kombination aus Merkmalen der hohen Spezialisierung (drei nach vorne zu vom Parietalloch gelagerte Zonen) und des Merkmals der Primitivität (Wachstumszone in der postpinealen Schädelpartie) resultieren würde. Ausserdem verdrängt die Zone des intensiven Wachstums in der Occipitalregion des Schädels die Articulatio mandibularis nach hinten nicht; wie dies an der Schädelbasis von *Diplocaulus magnicornis* und *Diceratosaurus punctolineatus* (s. B und E, Abb. 32) gut zu ersehen ist und verlängert somit den Kieferapparat des Tieres nicht. Folglich hätte die neue Wachstumszone bei *Lonchorhynchus*, dessen gesamte Specialisierung auf die maximale Verlängerung der Kiefer gerichtet ist, im wesentlichen nichts verändert und dem Tiere von keinem Nutzen gewesen.

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Wenn wir nun die oben besprochenen Fragen und Erörterungen in Kürze überblicken, so gelangen wir in bezug auf die Dermalknochen des Stegocephalen-Schädels zu folgenden Ergebnissen.

1. Die Deckknochen des Schädels vieler Stegocephalen können in zwei Gruppen eingeteilt werden: Knochen, die gleichmässig wachsen und Knochen, die eine Zone des intensiven Wachstums besitzen. Im ersten Falle erweitert der Knochen im Wachstumsvorgange gleichmässig nach allen Seiten sein Areal und seine äussere Oberfläche wird mit runden Waben bedeckt; im zweiten verfügt der Knochen in einigen Bezirken über ein gesteigertes Wachstum, das sich in einer bestimmten Richtung orientiert. An diesen Bezirken bilden sich statt runder Waben langgestreckte Rinnen und längliche Kämme. Das Zentrum des rundwabigen Skulpturbezirks entspricht stets bei sämtlichen Deckknochen des Schädels genau dem Ossifikationszentrum des Knochens. Infolgedessen bezeichnen wir die Region der runden Waben an der Knochenoberfläche als „zentrale Zone".

2. Die Zonen des intensiven Wachstums der einzelnen Knochen im Stegocephalen-Schädel bilden die Zone des intensiven Wachstums des Schädels in der Totalität. Derartige Zonen können im Schädel mehrere (höchstens drei) sein.

Die Zonen des intensiven Wachstums verändern stark die Gesamtumrisse des Schädels, zumal die Anordnung der Augen- und Nasenlöcher im Schädeldach. Bei verschiedenen Spezies der Stegocephalen ist die Anzahl und die Lokalisierung der Zonen des intensiven Wachstums verschieden; infolgedessen können sämtliche Vertreter der Stegocephalen, die Zonen besitzen, in eine Reihe von Gruppen und Typen eingeteilt werden.

3. Die Zonen des intensiven Wachstums modifizieren die Schädelform sowohl im Vorgange der phylogenetischen, als in demjenigen der individuellen Entwicklung der Stegocephalen. Bei der phylogenetischen Entwicklung dienen die Wachstumszonen gleichsam als Mittel, vermöge dessen der Stegocephalen-Schädel sich im Vorgange der Adaptation des Tieres seinen Existenzbedingungen verändert. Bei der individuellen Entwicklung bildet die Zone (resp. Zonen) des intensiven Wachstums den Schädel des Stegocephalen nach dem der entsprechenden Gattung eigenen Typus aus.

4. Die Knochen der vorderen Partie der Schädelbasis des Stegocephalen reagieren auf das Schädelwachstum mit einem gesamten, nicht lokalisierten, Wachstum. Die Knochen der hinteren Partie der Basis cranii bilden infolge ihrer Verbindung mit der Kaumuskulatur einen wenig veränderlichen Komplex. Der Bau dieses Komplexes wird von den Zonen des intensiven Wachstums des Schädels kaum beeinflusst.

5. Aus demselben Grunde erweist sich als wenig veränderlich auch der hintere Abschnitt des Unterkiefers. Dessen vorderer Abschnitt wächst entsprechend dem Gesamtwachstum des Schädels. Die Zahl und der Typus der Anordnung der Zonen des intensiven Wachstums im Schädel beeinflusst nicht die morphologischen Eigentümlichkeiten des Unterkiefers. Letzterer ist bei sämtlichen Spezies der Stegocephalen von fast gleicher Form.

6. Mit Ausnahme einiger Besonderheiten im Verlaufe des Sulcus jugularis bei manchen Formen aus dem Karbon, erstrecken sich die Furchen des Schleimkanals bei sämtlichen Stegocephalen an den gleichnamigen Knochen.

Die an der äusseren Knochenoberfläche gelagerte Furche überschneidet obligatorisch dessen Ossifikationszentrum. Der Schleimkanal ändert diese seine Beziehungen zu den Knochen und deren Ossifikationszentrum nie, welche immer die Schädelform des in Betracht kommenden Stegocephalen auch sein mag. Die Zahl und der Typus der Anordnung der Zonen des intensiven Wachstums stört nie die Beziehungen des Schleimkanals und dessen Furchen zu den Ossifikationszentren der Deckknochen des Schädels. Die Wachstumszonen die die Schädelform, die Lage der Augen- und Nasenlöcher usw. modifizieren, verändern lediglich das Gesamtbild des Verlaufs der Furchen des Schleimkanals. Dies findet in der Verschiebung der Knochen und in der Veränderung der Lagerungsstelle der Ossifikationszentren, mit welchen der Schleimkanal in Verbindung bestehen bleibt, seine Erklärung.

7. Sämtliche Stegocephalen, die keine Zonen des intensiven Wachstums in ihren Schädelknochen besitzen, haben einen kurzen und breiten Schädel. Einen gleichen Schädel besitzen auch die Larvenformen der Stegocephalen. Entfernt man sämtliche Zonen des intensiven Wachstums der Deckknochen des Schädels bei einem beliebigen erwachsenen hochspezialisierten Stegocephalen und setzt man den Schädel auf künstliche Weise bloss aus den zentralen Zonen dessen Knochen zusammen, so kommt ein kurzer und breiter

Schädel zustande, der einerseits mit dem Schädel der der Wachstumszonen ermangelnden Stegocephalen, andererseits mit dem Larvenschädel Ähnlichkeiten besitzt. Dies weist anscheinend darauf hin, dass sämtliche Labyrinthodonten ihren Ursprung der gemeinsamen kurzköpfigen primitiven Ausgangsform verdanken. Ihren morphologischen Eigentümlichkeiten zufolge stand diese Urform wahrscheinlich dem *Pelosaurus* oder *Branchiosaurus* sehr nahe. In Anbetracht einiger Merkmale waren die Vorfahren von *Lepospondyli* und *Adelospondyli* weitaus mehr primitiv organisiert; deren Schädel besassen einige den *Crossopterygii* eigenen Besonderheiten.

Die den Schädel ausbildenden Zonen des intensiven Wachstums stellen keine ausschliessliche Besonderheit der Stegocephalen dar. In einer geringeren Mannigfaltigkeit der Anordnungstypen und in geringerer Anzahl sind sie auch bei den Vertretern anderer Klassen der Wirbeltiere vorhanden.

In der vorliegenden Arbeit haben wir uns lediglich mit dem Stegocephalen-Schädel befasst. Die Ergebnisse der Erforschung der Zonen des intensiven Wachstums bei den anderen Wirbeltieren werden den Gegenstand einer gesonderten Mitteilung bilden.

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NACHTRAG ZUR KORREKTUR.

Nachdem ich diese Arbeit an die Redaktion abgesandt hatte, erhielt ich einige Arbeiten über Stegocephalen. Das veranlasst mich einige von ihnen kurz zu erwähnen. In der Ende 1934 veröffentlichten Arbeit „Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocephalien und Reptilien" (Zeitsch. f. Anat. u. Entw., Bd. 103) befasst sich W. Gross sehr kurz mit der Frage über den mikroskopischen Bau der Deckknochen des Schädels des *Mastodonsaurus* und des *Plagiosaurus*. Unsere Beobachtungen bestätigen vollkommen den entsprechenden Daten von Gross. Gross hat den Schichtbau der Knochen und den Befund eines Netzes feiner Kanäle in den Tuberkeln der Skulptur hervorgehoben. Die Beobachtungen von Gross erlauben uns anzunehmen, dass der mikroskopische Bau der Deckknochen des Schädels anscheinend bei allen Stegocephalen gleich ist.

Bei der Beschreibung der Schädel der Stegocephalen erwähnt Säve-Söderbergh in seiner Arbeit „On the dermal bones of the head in Labyrinthodont Stegocephalians and primitive Reptilia" (Meddelelser om Grønland, Bd. 98, 1935) manchmal auch, dass der Schleimkanal das Zentrum der Verknöcherung mancher Deckknochen durchkreuzt. Dabei aber zieht er keine Schlussfolgerung aus seinen Beobachtungen. Beim Vergleich der Schädel des *Capitosaurus* und des *Metoposaurus* fiel Säve-Söderbergh folgendes auf. Die einzelnen Gebiete des Schädels unterschieden sich nach ihrer Grösse. Er empfahl dafür eine

entsprechende Terminologie, gab dabei aber keine Erklärung diesen Eigentümlichkeiten der Schädelproportionen. Von grossem Interesse sind die von SÄVE-SÖDERBERGH beschriebenen *Lyrocephalus kochi* die zu den neuesten Funde in Grönland gehören. Im Gegensatz zum *Lyrocephalus euri* durchkreuzt der Sulcus jugalis des Schleimkanals bei dieser Gattung das Verknöcherungszentrum des Squamosum, was bei manchen karbonischen Formen und bei *Dwinosaurus* beobachtet wird. Diese Eigentümlichkeit des *Lyrocephalus kochi* erfordert spezielles Studium, weil bei Stegocephalen der Perm und der Trias der Sulcus jugalis sich gewöhnlich längs der Naht zwischen dem Squamosum und dem Quadratojugale befindet.

In seiner letzten Arbeit „Description of a collection of associated skeletons of Trimerorhachis" (Contrib. from the Museum of Paleontology, Vol. IV, 1935) erwähnt E. C. CASE bei der Beschreibung eines neuen Fundes von *Trimerorhachis*-Schädeln die Anwesenheit des Kiemenapparates bei einigen Exemplaren, gibt aber nicht an bei welchen. Dieses gibt uns leider nicht die Möglichkeit die Richtigkeit unserer Annahme über den Zusammenhang der Veränderung der Knochenskulptur mit der Metamorphose der Stegocephalen zu prüfen.

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EVOLUTION OF THE WING-PATTERN IN PALAEARCTIC SATYRIDAE

III.

PARARGE AND FIVE OTHER GENERA

BY

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With 11 figures in the text and 8 plates.

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INTRODUCTION.

The present paper is the third part of investigation upon the wing-pattern of the nine genera of palaearctic Satyrid butterflies. Its two preceding parts deal one with *Satyrus* and *Oeneis* (1929 a) and another with *Melanargia* (1931). In this part the remaining six genera are described, viz. *Pararge*, *Epinephele*, *Aphantopus*, *Erebia*, *Coenonympha* and *Triphysa*.

As it has been pointed out in the first named paper the purpose of the investigation is to find out whether the prototype of the wing-pattern constructed by the author (1924) for Nymphaloid families of butterflies, or using another terminology for Nymphalidae *sensu lato*, is a satisfactory scheme to derive from it all the wing-patterns of such large groups as that consisting of the 9 above mentioned genera. In the two published parts of this investigation an attempt is made to show that the above question seems to be generally answered in positive sense with regard to *Satyrus*, *Oeneis* and *Melanargia*. We have now to consider six other genera from the same point of view.

Like the two preceding parts of the investigation on palaearctic Satyridae the materials for the present one have been obtained in the Zoological Museum of the Academy of Sciences in Leningrad, and I take the opportunity of expressing my thanks to Dr. N. J. Kusnezov, Keeper of the Lepidopterological Department of the Museum for his valuable help in my using the fine palaearctic part of the collection of the Museum. The terminology adopted in this paper as to the morphology of the wing does not differ from that in the two preceding ones. The essence of it is readily seen in the text-figure 1. Also the particulars as to the method of figuring specimens and so on do not differ from those given previously (1929 a, p. 562).

We will consider the six genera in the sequence given above and begin with *Pararge* accordingly.

CHAPTER I.

REALISATION OF THE NYMPHALOID PROTOTYPE IN THE GENUS PARARGE.

The Satyrid genus *Pararge* Hbn consists according to Seitz (1909) of 15 species which comprise 43 forms. It is thus not very rich but it undoubtedly belongs to the most typical genera of Satyrids with its pronounced mostly numerous eye-spots and with its modest coloration in which dark hues strongly prevail.

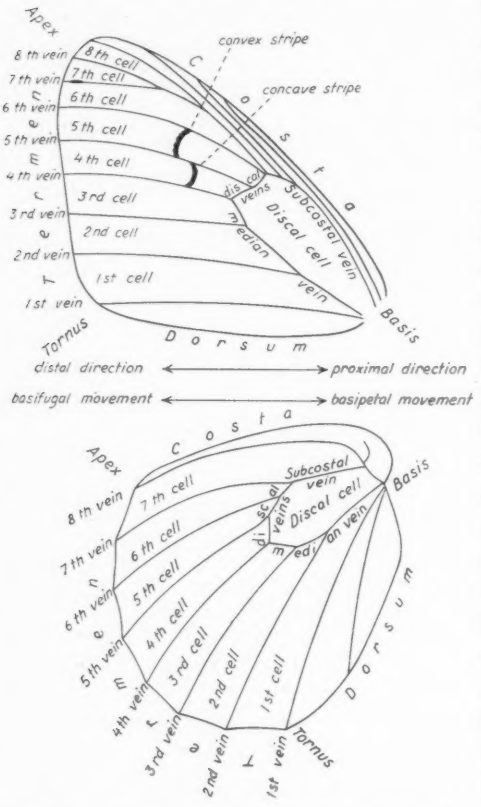

Fig. 1. Diagram explaining the terminology used in the present paper regarding morphology of the wing.

Let us consider now which is the connection of the genus with the Nymphaloid prototype and begin with a short description of the latter which runs as follows. The prototype of Nymphaloid patterns (text-fig. 2) is composed of a number of dark stripes and spots lying on a light ground. One part of them is transverse to the wing-veins, the other longitudinal to them. The transverse components are the following:—The first, second and third Externae (E^1, E^2, E^3) border the wing-margin. The series of eye-spots (OC) follows Externae. Each eye-spot is situated in a border or terminal cell, and is surrounded by a Circulus (C). The series of eye-spots is surrounded by the broad and diffused Umbra (U). The first and second Mediae (M^1, M^2) cross the middle area of the wing. The first and second Granulatae (G^1, G^2) are enclosed between them. The first Discalis (D^1) is placed between the Granulatae on the veins closing the discal cell. The second Discalis (D^2) and the Basalis (B) are situated proximally to the second Media. There are two categories of longitudinal components. The Venosae (V) cover the wing-veins; the Intervenosae (J) run between them. A formula of the prototype can be obtained by writing down the above indices in a definite sequence. Each eye-spot is designated in the formula

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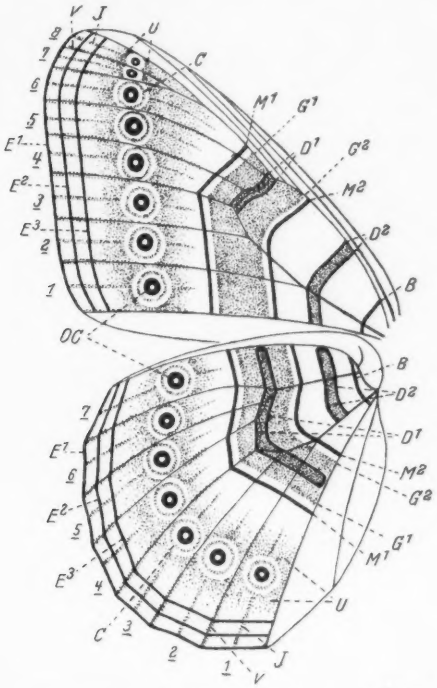

Fig. 2. The scheme or prototype of the wing-pattern of Nymphaloid families (Nymphalidae, Satyridae, Morphidae, Amathusiidae, Brassolidae). *B* Basilis, *C* Circulus, D^1 first Discalis, D^2 second Discalis, E^1 first Externa, E^2 second Externa, E^3 third Externa, G^1 first Granulata, G^2 second Granulata, *J* Intervenosa, M^1 first Media, M^2 second Media, *OC* eye-spot (another designation of eye-spots see below), *U* Umbra, *V* Venosa. The ciphers near the wing-margin designate numbers of border cells. The dash under the cipher designates the presence of an eye-spot in a given cell. The prototype corresponds to the formula:

$$\frac{E^1.\,E^2.\,E^3.\,OC\ (1.\,2.\,3.\,4.\,5.\,6.\,7.\,8.)\ U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}{E^1.\,E^2.\,E^3.\,OC\ (1.\,2.\,3.\,4.\,5.\,6.\,7.)\quad U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}$$

(SCHWANWITSCH, 1924.)

separately by the number of its cell. The Circuli are not included in the formula. The indices of the forewing are placed above the line, those of the hindwing below it. The formula of the prototype is the following:

$$\frac{E^1.\,E^2.\,E^3.\,OC\ (1.\,2.\,3.\,4.\,5.\,6.\,7.\,8.)\ U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}{E^1.\,E^2.\,E^3.\,OC\ (1.\,2.\,3.\,4.\,5.\,6.\,7.)\quad U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}$$

Pararge achine (fig. 2) shows a great number of components in its pattern which obviously correspond with those of the prototype. Three Externae (E^1, E^2, E^3) of a very regular, almost undisturbed form run along the termen of both wings. They are followed by the series of well developed mostly pupillated eye-spots which is very complete as the only absent members of it are those of the 7th cell on hindwing and of the 1st, 7th and 8th ones

on forewing. It should be remarked that the presence of an eye-spot in the given cell is designated by putting a line under the number of the latter in the figure. The eye-spots are surrounded by the Umbra (*U*) which has retained on the forewing its characteristic diffused margins. The first Media (M^1) is strong on both wings, almost so is the second Media (M^2) on the forewing, while only the discal portion of it is seen on the hind one. The first Discalis (D^1) is conspicuous on the forewing only, the second one (D^2) is well pronounced on the forewing, while on the hindwing principally its distal and anterior margins are seen the rest being merged into basifugal melanisation (*Bm*) by which name I have designated (1931, p. 371) the darkening of the ground of the wing which spreads basifugally (see the text-figure 1 for the meaning of the word) from the wing-basis. This melanised area is also seen on the forewing. On account of the above data the following formula of *achine* pattern may be given in which the absent components are indicated by dashes:

$$\frac{E^1.\,E^2.\,E^3.\,OC\,(-\,2.\,3.\,4.\,5.\,6.\,-\!-\!-)\;\;U.\,M^1.\,M^2.\,-\!-\,D^1.\,D^2.\,-\,|\,-\!-}{E^1.\,E^2.\,E^3.\,OC\,(\,1.\,2.\,3.\,4.\,5.\,6.\,-)\quad U.\,M^1.\,M^2.\,-\!-\!-\,D^2.\,-\,|\,-\!-}$$

15 indexes of pattern components are absent in this formula out of 41 composing the formula of the prototype. But some of components not found in *achine* pattern have been discovered in other species of *Pararge*.

On the forewing of *Pararge tigelius* (fig. 3) well developed pupillated 6th and 7th eye-spots are present the latter of which does not exist in *achine*. The next two specimens belonging to *maera* (figs. 4, 5) are remarkable in their having eye-spots in the 8th cell of the forewing. The eye-spots are very small but sufficiently pronounced and pupillated. The interest of their presence lies in the fact that the 8th eye-spot is generally not a common component in Nymphaloid families while in Satyridae it has not been recorded at all but in *Pararge maera*. The pattern formula of the family of Satyridae published by me in 1924 (p. 517) is:

$$\frac{E^1.\,E^2.\,E^3.\,OC\,(1.\,2.\,3.\,4.\,5.\,6.\,7.\,-)\;\;U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}{E^1.\,E^2.\,E^3.\,OC\,(1.\,2.\,3.\,4.\,5.\,6.\,7.)\quad U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}$$

The 8th eye-spot of the forewing is absent in it as before the publication of that paper the *maera* case was not known to me. Now after adding the index of the missing component to the above formula that of Satyridae runs as follows:

$$\frac{E^1.\,E^2.\,E^3.\,OC\,(1.\,2.\,3.\,4.\,5.\,6.\,7.\,8.)\;\;U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}{E^1.\,E^2.\,E^3.\,OC\,(1.\,2.\,3.\,4.\,5.\,6.\,7.)\quad U.\,M^1.\,M^2.\,G^1.\,G^2.\,D^1.\,D^2.\,B.\,|\,V.\,J.}$$

Thus it is absolutely complete like the formula of *Nymphalidae s. str.* (1924, p. 525). This completion of Satyrids formula on the basis of *Pararge* pattern has been described already in one of my notes in Russian (1927, p. 98).

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Returning now to *Pararge* itself the hindwing of *Pararge roxelana* should be mentioned (fig. 9) in which the 7th eye-spot is very strong and pupillated thus completing our initial *achine* pattern. From the above data the following eye-spots formula may be derived for the genus *Pararge:*

$$\frac{OC\ (-2.3.4.5.6.7.8.)}{OC\ (1.2.3.4.5.6.7.)}$$

The only eye-spot absent in it is the 1st of the forewing. It should be remarked here that this particular eye-spot does not belong to rareties. It has been recorded e.g. in *Satyrus* (1929 a, p. 567) which genus is generally much poorer in eye-spots than *Pararge* for which reason it does not seem unlikely that it may be discovered in some fresh *Pararge* materials.

As to the Umbra (*U*) it is quite prototypical on the forewing of *achine* while on its hindwing regular circles have evolved from the component. But in *Pararge eversmanni* (fig. 53) the diffusion of the *U* margins is no less characteristic than in the prototype.

Passing now on to the more proximal components the forewing of the same species should be examined (fig. 6). Its first Media (M^1) does not show basifugal dislocation so typical of the anterior part of *achine* M^1 thus not differing substantially from the prototype. All the components located in the discal cell are very fine in fig. 6 (D^1, M^2, D^2) including Basalis (*B*) which stripe is absent in *achine*. On the hindwing of *Pararge megera* (fig. 7) the first Media (M^1) shows a very prototypical form, while the second one (M^2) is seen in its total length which is not the case in *achine*. Also the first and second Discalia (D^1, D^2) are well pronounced thus surpassing *achine* in their resemblance to the prototype. In *Pararge tigelius* (fig. 8) a shadow-like dark field between the Mediae is present, the margins of which most likely correspond to Granulatae (G^1, G^2). Now in *Pararge thibetanus* (fig. 32) a component is seen in the 7th cell (*B*) which may be either anterior part of Basalis or the same of the second Discalis. The former alternative seems more plausible, as firstly the component in question is placed too proximally to derive it from the same source as the two undoubted fragments of D^2 lying in the discal cell; secondly all the margins of the latter component are equally sharp cut, while in the marking in question such is only the distal border, the proximal one being diluted and thus a difference existing in fig. 32 between D^2 and *B* with regard to their structure. Hence I think it right to accept the existence of Basalis in the 7th cell of *Pararge* hindwing. Finally rather typical Venosae (*V*) are seen on the forewing in *Pararge sicula* (fig. 43) and on the hindwing in *Pararge egeria* (fig. 39).

Let us now summarize the formula of *Pararge achine* and the formulae of some of the just considered specimens taking the latter only in their parts which are of interest for us.

Pararge achine (fig. 2).

$E^1.\ E^2.\ E^3.\ OC$ (— 2. 3. 4. 5. 6. — —) $U.\ M^1.\ M^2.$ — — $D^1.\ D^2.$ — — —

$E^1.\ E^2.\ E^3.\ OC$ (1. 2. 3. 4. 5. 6. —) $U.\ M^1.\ M^2.$ — — — $D^2.$ — — —

Pararge maera (fig. 4).

OC (4. 5. 6. 7. 8.)

Pararge roxelana (fig. 9).

OC (5. 6. 7.)

Pararge megera (fig. 7).

$M^1.\ M^2.$ — — $D^1.\ D^2.$

Pararge tigelius (fig. 8).

$M^1.\ M^2.\ G^1.\ G^2.$

Pararge eversmanni (fig. 6).

$M^1.\ M^2.$ — — $D^1.\ D^2.\ B.$

Pararge thibetanus (fig. 32).

$B.$

Pararge egeria (fig. 39).

$V.$

$V.$

Protopararge (fig. 1).

$E^1.\ E^2.\ E^3.\ OC$ (— 2. 3. 4. 5. 6. 7. 8.) $U.\ M^1.\ M^2.$ — — $D^1.\ D^2.\ B.\ |\ V.$ —

$E^1.\ E^2.\ E^3.\ OC$ (1. 2. 3. 4. 5. 6. 7.) $U.\ M^1.\ M^2.\ G^1.\ G^1.\ D^1.\ D^2.\ B.\ |\ V.$ —

This summarized formula shows the total of the components of the prototype which have been found in the representatives of the genus *Pararge* and may be therefore called generic formula. On the basis of it a hypothetical pattern is constructed which deserves the name of Protopararge (fig. 1). Its resemblance to the prototype exhibits better than any wordy explanation how close is the connection of the genus in question with the prototype. It should be pointed out here that the generic formula of *Pararge* consists of 36 components, thus only 5 out of 41 components of the prototype being absent in it. This may be called a very complete realisation of the prototype as *Pararge* with its 36 components surpasses greatly other palaearctic genera like e.g. *Satyrus* in which I was able to discover only 27 components in spite of the fact that the last named genus is much more superior than *Pararge* as to the number of species. Besides this it should be noted that four of the components absent in *Pararge* are generally not very frequent and not very important. Such are the Intervenosae (J) and the forewing Granulatae (G^1, G^2). The forewing 1st eye-spot is more frequent but the probability of its discovering is already referred to (p. 149).

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CHAPTER II.

MODIFICATIONS OF THE WING-PATTERN ON THE UNDERSIDE OF PARARGE.

In the present chapter we have to consider the most interesting modifications which the components of the prototype undergo on the underside of wings in *Pararge*. We begin with the Externae.

§ 1. EXTERNAE.

A. Disappearance of the second Externa.

It has been shown in my previous publications that the second Externa is strongly inclined to disappear while the two other Externae mostly remain unaltered, and thus a bi-striped condition arises on the termen. The disappearance of the second Externa is due either to its elimination or to coalescence with the first Externa. Both indicated ways have been recorded by me in both *Satyrus* (1929 a, pp. 571, 572) and *Melanargia* (1931, p. 326). Also in *Oeneis* the stripe in question is absent (1929 a, p. 626).

In *Pararge* the second Externa is generally more stable than in the above mentioned genera. But e.g. on the hindwing upperside of *megera* (fig. 37) the first and second Externae have almost fused into a single stripe $E^1 + E^2$. In *Pararge thibetana* (fig. 35) the same fusion has become complete on the underside. On the forewing of another *thibetana* specimen (fig. 28) the complex stripe $E^1 + E^2$ has undergone degeneration and almonst vanished from the posterior cells. Thus the disappearance of the second Externa is sufficiently pronounced in *Pararge*. The correctness of the above homologisation will be discussed in the conclusive paragraph of the present chapter.

B. Forms of cell-portions.

The cell-portions of the third Externa may acquire different shapes. Concave and convex ones are the most important of them and their more detailed classification is given in my paper on *Melanargia* (1931, p. 328). One of singular forms, namely that designated as convex bi-arcuate, is very characteristic of *Pararge*. It may be seen in figs. 15, 36 (E^3) and it is interesting that also the second Externa (E^2) is shaped in the same way in the indicated figures though in a less degree. This sort of behaviour is generally less common in E^2 than in E^3. The modification called bracket-like modification is exemplified in *Pararge episcopalis* (fig. 34) where like the preceding case both E^3 and E^2 are modified in one direction

(cf. the 3rd cell on the hindwing). Rather typical concave cell-portions are existing in the third Externa of *roxelana* (fig. 9) while in *deidamia* (fig. 30) the same tendency manifests itself in the second Externa (E^2). Thus several modifications of Externae previously described in *Satyrus, Oeneis* and *Melanargia* occur in *Pararge* as well.

C. Fragmentation of the third Externa.

In my preceding publications a number of cases are described of the division of different stripes into parts, mostly into cell-portions. In the majority of them the process is connected with and dependent upon, the dislocations of the respective cell-portions. The third Externa on the hindwing of *Pararge thibetana* is one of the examples of division (E^3 in fig. 35) and it should be remarked that the cell-portions resulted in are uncommonly broad and heavy. But besides this broadening the interest of *thibetana* E^3 lies in the fact, that the indicated cell-portions follow exactly the line where an uninterrupted third Externa would pass, and do not dislocate in any direction. It is evident that the division is due to the elimination of dark pigment from the narrow areas running along the veins, or in other words to some shortening of the cell-portions in question. I should offer to name serial fragmentation the just described form of division, meaning by this that a stripe can dissolve into regular series of fragments owing to the breaking off of its respective parts from each other *in loco*, without any influence of dislocation on the final result of the process. The same modification occurs on the forewing. On comparing E^3 of the forewing in fig. 35 with its homologue in fig. 28 ($E^3$3, $E^3$4, $E^3$6, $E^3$7) it is readily seen that the stripe nearly continuous in the former has undergone typical fragmentation in the latter.

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§ 2. EYE-SPOTS.

Some of the modifications observed in the eye-spots of *Pararge* represent considerable interest.

A. False Circuli.

The modification to be dealt with in the present section is of a rather singular sort.

On the hindwing of *Pararge megera* v. *lyssa* (fig. 12) which is figured under considerable magnification a fine series is seen of black eye-spots, each of them being provided with a bright white pupil. The most remarkable pecularity of them is that they are surrounded by a pair of concentric circles each. E.g. in the 3rd cell the indicated circles are designated the exterior by

$C3$ and the interior by $pOC3$ while the component which seems to be eye-spot properly is designated as $cOC3$. In all the other cells of the hindwing exactly the same status is ready to see. As to the exterior circles they undoubtedly correspond to the Circuli of the prototype (*C* in text-fig. 2, p. 147) and consequently owe their origin to the condensation of the "mass" of Umbra round the eye-spots. The indicated derivation of Circuli has been elucidated in one of my preceding papers (1929 b, p. 48) and in the present case its correctness is supported by the fact of the peripheric margins of $C3$ being markedly suffused. In other cells in fig. 12 the condition is the same, and particularly in the 5th and 6th ones the exterior circles and the slightly granulated Umbra (*U*) are not quite separated from each other.

But the homology of interior circles, i.e. of $pOC3$ and its homologues is much more difficult to establish. Two alternatives are equally possible if considering the hindwing only. Either the interior circles, like the exterior ones, originate from the Umbra and in such a case the Circuli of the prototype should be supposed to exist in double number. Or the interior circles represent a derivative from the eye-spots. To solve this problem let us turn attention to the forewing, and begin with its anterior cells in *Pararge megera* (fig. 10). Two of its eye-spots are of importance for us, the large 5th one ($OC5$) and the small 6th one ($OC6$). Both of them are pupillated and each is surrounded by its own Circulus ($C5$ and $C6$ resp.), the latter being partly fused with each other owing to their close position, and being not quite segregated from the Umbra (*U*). There is no doubt whatever that $C5$ and $C6$ are genuine homologues of the Circuli of the prototype. The great eye-spot $OC5$ is totally black except for its large white pupil. Different is the case in $OC6$. The greater part of it is also black, but its margin near the lower end of the pointing line is considerably lighter than the rest and shows brownish coloration.[1]

Passing now on to *Pararge maera* v. *adrasta* (fig. 11) we observe the same phenomenon in the large eye-spot (OC (4. 5)) which has arisen from the fusion of the 4th and 5th eye-spots. The peripheric zone of this double eye-spot has become brownish on its whole circumference, while the wide central area remains as black as the total of $OC5$ in fig. 10. It is obvious that the process of lightening begun in the anterior part of $OC6$ in fig. 10 has spread over the total periphery of OC (4. 5) in fig. 11. A still further advancement of the process shows the eye-spot situated in the 6th cell in fig. 11. Except for its white pupil nearly the total of it has become brownish. Only tiny remnants of black ($cOC6$) are conspicuous near the pupil. Passing now on to the same eye-spot in *lyssa* (fig. 12) we see some more details. Its white pupil is encircled by the narrow black line $cOC6$. The latter

[1] Owing to the process of reproduction the difference between the brown and black parts of large eye-spots is less visible in figs. 10, 11 than in the original drawings.

is surrounded by the broad brownish zone, but what is the most important, the very periphery of the latter (*pOC6*) is considerably darker than the rest. The whole system is encircled by a typical Circulus (*C6*). It should be pointed out here, that in the figure 11 the rudiment of the darkish peripheric zone can be also recognized (*pOC6*) but in a less distinct form. It is thus evident that the lightening in fig. 12 leaves intact the central area of the 6th eye-spot (*cOC6*), develops most strongly in the surrounding subperipheric zone and is somewhat less pronounced on the periphery (*pOC6*) of the eye-spot.

On comparing now the 6th forewing eye-spot of *lyssa* (fig. 12) with its numerous hindwing homologues, it becomes clear that the latter show the same modification in a more pronounced form. Obviously the black *cOC3* of the hindwing corresponds to *cOC6* of the forewing being only larger, the dark brown brim *pOC3* is homologous with *pOC6* being only much stronger, and finally the broad light interspace between *cOC3* and *pOC3* does not differ substantially from that between *cCO6* and *pOC6*. Also the correspondence of Circuli (*C3* and *C6*) is quite doubtless. Consequently the black pigment has disappeared from the hindwing eye-spots of *lyssa* with the exception of their central areas (*cOC3*), the latter giving the impression of genuine intact eye-spots, which interpretation we have temporarily admitted in the beginning of this section. The lightening in the comparatively broad subperipheric zones of eye-spots is much stronger than in the narrow peripheric ones. It is now easy to understand why the interspace between *pOC6* and *cOC6* in fig. 12 is somewhat darker than that between *cOC6* and *C6*. The former is a part of lightened eye-spot, the latter represents a true interspace between two prototypical components. On the hindwing the indicated distinction is less pronounced but conspicuous yet.

The described modification results in an undeniable resemblance of the segregated peripheric zones of eye-spots to prototypical Circuli, and it seams reasonable to designate the newly formed components in question as false Circuli. The above analysis shows that the false Circuli and the prototypical Circuli have nothing in common, as the former originate from the eye-spots while the latter derive from the Umbra.

This homologisation has been briefly referred to in my short note of 1927 (p. 98). Later on in my paper on South American Nymphalids *Prepona* and *Agrias* (1930, p. 331) some data were published upon quite similar lightening of eye-spots in the former genus without formation, however, of false Circuli. Also in the African Satyrid *Leptoneura clytus* L. the same modification is observed, so that the case of *Pararge* does not stand alone. But undoubtedly in *Pararge* its most interesting form takes place.

Besides this the fact should be emphasized that in the forewing only the anterior eye-spots have lost their black, while the 5th and the 4th ones (*OC4*,

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*OC*5) either have not altered at all (figs. 10, 12), or have done so but slightly (fig. 11). Exactly the same is seen in figs. 4, 5, while in fig. 14 even the 6th eye-spot is unmodified, and only the 7th one shows typical false circle. Consequently only the most anterior forewing eye-spots modify themselves in accordance with their hindwing homologues, whereas the more posterior ones do not. This is, however, the result of a more general phenomenon named by me Oudemans' rule (1931, p. 390). The latter will be discussed more particularly in Chapter XVII, and here I restrict myself to pointing out that the said rule covers the cases when the total of the hindwing and the apical area of the forewing (on the underside only) show the same type of color-pattern, while the rest of the forewing, where exactly the unmodified eye-spots are placed in *Pararge*, exhibits another type of color-pattern. Thus from the standpoint of Oudemans' rule the existence of the two types of eye-spots on the forewing is quite normal.

B. Ereboid dislocation.

In my paper on *Satyrus* a peculiar modification in the eye-spots has been described which consists in "a basipetal dislocation of the 4th and 5th eye-spots of the forewing—or sometimes of the 5th only—in such a way as to make the anterior end of the chain of eye-spots characteristically sinuous" (1929 a, p. 530). This modification has been named ereboid or parargoid owing to its typical manifestation in *Erebia* and *Pararge*. No materials have been published yet concerning the modification in question in the indicated genera, but now it is easy to see the development of the process, in the last named genus.

In *Pararge achine* (fig. 13) the eye-spots are numerous and follow a line more or less parallel with the termen.

In *Pararge hiera* (fig. 14) the eye-spots series is also very complete but their positions differ from those in *achine*. The large eye-spot lying in the 5th cell is markedly shifted basipetally compared to that of the 6th cell, while just the opposite is the case in the preceding figure. The 4th eye-spot of *hiera* is shifted in the same direction as the 5th one, but in a less degree. Thus the line of eye-spots going straight in fig. 13 has become curved inwards in the 4th and 5th cells in fig. 14, the maximum development of the modification being restricted to the 5th cell, while the 4th eye-spot gives the impression that it only tends to join the strongly dislocating 5th one, not being, however, very successful.

In *Pararge megera* (fig. 15) the 5th eye-spot has advanced still more basipetally, and e.g. the distance of its white centre from the small 6th eye-spot has increased much compared with the preceding figure. The 4th eye-spot of *megera* has also dislocated, but again not so far as the 5th one. This

difference between the two eye-spots with regard to the degree of their dislocation seems to be a rule in *Pararge*. Its numerous examples may be easily seen in the plates I and II though in some cases the 4th eye-spot follows the 5th one very closely (fig. 12).

Thus the ereboid curvation of the eye-spots series is very simple to observe. But remarkable is the constancy of this modification in palaearctic Satyridae. Besides *Satyrus* I have recorded it in *Oeneis* (1929 a, p. 630) and we shall see it in almost all the remaining genera dealt with in the present paper.

Besides the erebisation on the forewing we meet in Pararge with a dislocation in the hindwing eye-spots that may be considered as a counterpart of the former process. In *Pararge eversmanni* (fig. 53) the four posterior eye-spots form a roughly straight line so located that the 4th eye-spot lies far form the first Media. Meanwhile the 5th eye-spot is situated very near by the indicated stripe, and almost the same is the position of the 6th one. Thus the 5th eye-spot has shifted basipetally from the more or less stationary 4th one which circumstance represents one of the typical characters of erebisation as observed on the forewing. It should be noticed that the 6th eye-spot is shifted like the 5th one that not being so in the typical forewing process. The whole of the above evidence allows, I believe, to term the described modification as erebisation on the hindwing though in a form not exactly corresponding with that of the forewing. On the other hand it is noteworthy that in the hindwing of *Erebia* itself the process has not been recorded.

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C. Combinations.

Elimination of many eye-spots from the wing-pattern represents one of the most common ways of the evolution of the prototype, and the combinations of the eye-spots left are often very characteristic.

Pararge belongs to genera with numerous eye-spots particularly in the hindwing. Very polynome series are not uncommon in the genus, like that seen on the hindwing of *achine* (fig. 2) in which the 7th eye-spot is the only absent member. *Pararge megera* (fig. 12), *episcopalis* (fig. 34), *thibetana* (fig. 35) and *eversmanni* (fig. 53) though being widely differing from *achine* and from each other in the general character of their patterns all exhibit nevertheless exactly the same hindwing formula *OC* (1. 2. 3. 4. 5. 6. —) as the last named species. With regard to this *Pararge* stands close to *Melanargia* for which genus the above written formula has been also found typical (SCHWANWITSCH, 1931, p. 335).

On the forewing of *Pararge* the eye-spots series is less complete particularly in the posterior cells, so that the 1st eye-spot which is generally rather common has not been discovered in the genus at all. But this is compensated, so to say, by the completeness of the anterior part of the series, where the

rare 8th eye-spot is present (figs. 3, 5). As to the relative stability of the forewing eye-spots, the 5th one is undoubtedly the most constant of them; it is often present when all the others have vanished. This occurs both on the underside (figs. 31, 34, 35, 53) and on the upperside (figs. 38—41, 46, 50, 51, 52), the latter case being especially typical. The greater stability of the 5th eye-spot compared with the rest of them is obviously dependent upon its large size, which makes the eye-spot in question markedly predominating even if some others are present as well (figs. 15, 36, 37). This property of the 5th forewing eye-spot of *Pararge* evidently belongs to intergeneric tendencies as exactly the same has been recorded by me in *Satyrus* (1929 a, p. 584) and *Melanargia* (1931, p. 335). Curiously enough the 4th eye-spot of the forewing seems tending to reach the condition of the 5th one in both its position and size. The former tendency has been illustrated in the preceding section, the latter is readily seen in figs. 11, 12, 14, 43, 44.

On the basis of the above data we can say that the eye-spots formulae $\frac{OC(---4.5.---)}{OC(\ 1.2.3.4.5.6.-)}$ and $\frac{OC(-----5.---)}{OC(\ 1.2.3.4.5.6.-)}$ represent a status which occurs in *Pararge* not unfrequently. If it is not exactly realised a strong tendency to its realisation may be often seen. The fact should be emphasized that the typical eye-spots formulae of *Melanargia* are just the same (l.c. ibid.). Meanwhile *Satyrus* shows quite a different type in the evolution of its eye-spots series characterised by the formula $\frac{OC(-2.--5.---)}{OC(-2.-----)}$, the latter being very oligonome (SCHWANWITSCH, 1929 a, p. 584). Also *Oeneis* being very multiocellar genus has, however, its own typical combinations differing from those of *Pararge* and *Melanargia*. The two last named genera concerning their eye-spots are undoubtedly closer to one another than to any other genus of palaearctic Satyrids.

§ 3. MEDIAE AND DISCALIA.

The first and second Mediae are perhaps more liable to modifications than any other components of the prototype. *Pararge* shows some interesting examples in this direction.

A. Pierellisation of the second Media.

The remarkable process of pierellisation owes its name to South American Satyrid *Pierella* in which it was first discovered (SCHWANWITSCH, 1925). In the same genus and in some closely related ones pierellisation reaches its most characteristic form. The process may be described as "principally the basipetal dislocation of the postdiscal portions of the first and second Mediae

and the basifugal dislocation of the discal portion of the second Media" (SCHWANWITSCH, 1929 a, p. 643). Very often, however, this modification is restricted only to the second Media of the forewing, while the first Media on the same wing and both Mediae on the hind one remain unaffected. Just the indicated form of pierellisation is observed in *Pararge*. Let us follow its gradual development.

In *Pararge hiera* (fig. 16) the second Media crosses straight the discal cell (M^2) but before to enter the 2nd cell it turns basipetally along the median vein, so that the postdiscal portion of the stripe is placed a little more proximally than the discal one. But the general course of the component is rather strait.

In another *hiera* (fig. 17) the described dislocation has much advanced and the postdiscal portion of the second Media ($M^2 1$) has nearly reached the level of the second Discalis (D^2). As it is usual in such cases (SCHWANWITSCH, 1928 a, fig. 8; 1929 a, fig. 57; 1931, fig. 38) one observes readily that the basipetally directed hind part of the stripe ($M^2 4$) diminishes steadily towards its end, and thus tends to break off from its $M^2 1$ portion.

In *Pararge menava* (fig. 18) the expected rupture is a fact, no connection of $M^2 4$ with $M^2 1$ can be more seen, as the above mentioned basipetally directed end of the former has "contracted" and placed itself on the geometrical prolongation of the rest of $M^2 4$, that peculiar alteration being due to the elasticity of the component. The indicated contraction also reproduces fairly exactly the status described by me in *Satyrus* (1929 a, p. 588, fig. 58).

Finally in another specimen of *menava* (fig. 19) $M^2 1$ is placed exactly on the geometrical prolongation of D^2, so that without the above consideration the former component could be rather derived from D^2 than from its real maternal stripe M^2. This is also in accordance with the facts observed e.g. in *Pierella* or in *Caerois*.

Thus pierellisation of the second Media in the forewing of *Pararge* runs along the same lines as in other genera of Satyridae, and the above described form of the process is quite typical.

No pierellisation has been recorded in the first Media of *Pararge* though some inclination to it may be noted e.g. in fig. 16 where the M^1 position in the 3rd cell is more proximal than in the 4th one.

B. Coenonymphoid first Media.

In the first Media of *Satyrus* I have described a modification called coenonymphoid as it is very characteristic of the genus *Coenonympha*. It consists of the stripe in question becoming bent inwards in the 4th cell of the hindwing and subsequently entering the discal cell (1929 a, p. 599). Similar bending of the first Media is observed in *Pararge* patterns.

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One form of the process is exemplified by three specimens of *Pararge eversmanni*. In one of them (fig. 20) M^1 is continuous though markedly bent inwards in the 4th cell. In another (fig. 21) the increase in the indicated bending has led to breaking off of the 4th cell-portion from the 3rd one, and thus a peculiar course of M^1 is the result. In the third specimen (fig. 22) the described peculiarity is still more pronounced owing principally to the basifugal dislocation of M^1 in the 5th and in the anterior part of the 4th cells.

Somewhat different form of the same modification shows *Pararge deidamia*. In fig. 23 M^1 is nearly prototypical; in fig. 24 a very slight impression is conspicuous in the posterior part of the 4th cell; in fig. 25 the said impression is deeper; in fig. 26 still more so, and finally in fig. 27 M^1 forms a considerable "gulf" in the 4th cell. The principal difference of *deidamia* case from that of *eversmanni* is that in the former the total of the area proximal to M^1 undergoes melanisation so that in figs. 26, 27 M^1 represents but a boundary of the wide dark area.

Thus in both *eversmanni* and *deidamia* the hind part of the 4th M^1 cell-portion dislocates basipetally and an abrupt curvation or even interruption (in *eversmanni*) of the stripe is resulted in. The tendency is undoubtedly the same as in *Satyrus*, but it has been mentioned already that in the latter genus M^1 enters the discal cell. This is not the case in *Pararge*, but this difference between the two genera is not of importance as to the behaviour of pattern components and seems to be due to the different venation: in *Satyrus* the discal cell is rather long so that its apex lies closely to unmodified M^1 and even a small basipetal shifting of the latter brings it into the cell; in *Pararge* the discal cell is shorter and accordingly the dislocated M^1 does not reach it.

C. Melanargoid dislocation.

By melanargoid modification of the first Media the case is meant when on the forewing "the portion of M^1 lying in the 3rd cell dislocates basifugally while the portion of the 4th cell does the same basipetally. The result is that the two indicated portions come to lie far from one another, and thus the stripe becomes shaped ladder-like" (Schwanwitsch, 1931, p. 336). This modification is very typical of the genus *Melanargia* which its very name derives from, but its manifestation in *Pararge* may be easily demonstrated as well.

In *Pararge thibetana* (fig. 28) two lines are running from the upper index M^1, the left line points to the 3rd cell portion of the first Media, the right one points to its 4th and more anterior portions. It is obvious that the former is displaced in the distal direction while the latter has shifted in the proximal

one, so that the distance between the two has become very considerable, and thus the essential of melanargoid ladder-like dislocation is reproduced fairly well.

Two other modifications of Mediae in *Melanargia* already described should be mentioned here. One of them is the approximation of the discal portion of the second Media to the discal veins and its subsequent fusion with the anterior part of the first Media (l.c. p. 338). In fig. 28 M^2 is closely aproximated to the discal veins and fuses practically into a single broad band with the above described M^1. With few secondary distinctions this status reproduces that existing in *Melanargia*. Another modification often observed in the latter genus is a strong basifugal dislocation of the 1st cell-portion of the first Media and its approximation to the third Externa (l.c. p. 337). This may be again seen in *Pararge thibetana* (fig. 28, lower M^1 index) and a still more advanced condition shows *praecusta* (fig. 31) with its hind end of M^1 reaching nearly the wing-margin. The above description shows that *Pararge* and *Melanargia* are very similar in the modifications of their forewing first Media.

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D. Oblique dislocation of the first Media on the forewing.

The oblique dislocation of the first Media on the forewing was described by me first in the Eastern Satyrid *Lethe* (1926) and then recorded in *Satyrus* (1929 a, p. 585) and *Melanargia* (1931, p. 335). The essence of the modification is that M^1 of the forewing being roughly parallel to the termen in posterior cells of *Pararge achine* (fig. 2) becomes slightly oblique to it in *Pararge deidamia* (fig. 29) and markedly so in another *deidamia* (fig. 30). The same position of M^1 is seen in figs. 12, 16. Like *Satyrus* and *Melanargia* the modification in question does not reach its high degree in the indicated forms as in all of them the Ist cell-portion of the stripe is somewhat backward compared to the more anterior ones. This is not so in *Pararge episcopalis* (fig. 34). The hind end of its forewing M^1 has approximated the termen very closely. Therefore the total course of M^1 has become typically oblique, i.e. the component runs from the middle of the costa to the tornus. Besides this M^1 is considerably bent down. All this reminds the condition observed in *Lethe* very closely and thus with regard to the modification in question the genus *Pararge* as a whole stands higher than *Satyrus* and *Melanargia*.

E. Fragmentation of the Medial band.

The first and second Mediae being symmetrical stripes sometimes behave as a single component, so that it is convenient to describe the latter as Medial band. Several examples of division of the latter into parts have been de-

scribed by me in other palaearctic genera (1929 a, pp. 591, 600, 633; 1931, pp. 349, 352) and also in the South American Nymphalid *Prepona*. A peculiar case of this phenomenon has been discovered in *Pararge thibetana*.

In fig. 32 the Medial band (M^1, M^2) is rather widely interrupted in the 4th cell and respectively in the discal one almost exactly in the way described by me in *Satyrus* (1929 a, fig. 67). In other respects its character is quite normal though a constriction on the 7th vein should be noted. In another *thibetana* specimen (fig. 35) the said constriction has led to a total separation of the anterior part of the band ($M^1 + M^2$) from the middle one ($M^1 + M^2(4, 5)$). The latter now represents an irregularly oval marking widely distant from both $M^1 + M^2 7$ and the posterior part of the band (M^1, M^2). Its correct homologisation would be difficult without having fig. 32 at the disposal. Thus the Medial band has dissolved into three parts which process like that recorded in the third Externa of the same species (p. 152) well deserves the name of f r a g m e n t a t i o n. The two anterior fragments ($M^1 + M^2$, $M^1 + M^2(4, 5)$) are both characteristically short, the posterior one is much longer and shows undoubted tendency to a further fragmentation according to the number of cells crossed that tendency being partly dependent upon the white coloration of veins.

F. Division of the second Discalia.

In *Pararge hiera* (fig. 16) the second Discalis (D^2) represents a continuouse stripe. In another *hiera* (fig. 17) it has dissolved into three small markings. Also in *thibetana* D^2 on the forewing may be either continuous (fig. 35) or divided into anterior and posterior halves (fig. 28), the process, however, being evidently dependent upon a marked dislocation of the halves, which is not the case in *hiera*. Similar process takes place on the hindwing. In one *megera* specimen (fig. 7) D^2 is continuous, in another (fig. 8) it represents two independent spots which are dislocated like the above described of *thibetana* the anterior basipetally, the posterior basifugally. This condition is common in *Pararge* hindwings (figs. 20, 32). Similar divisions of D^2 also occur in some other genera as e.g. in the Nymphalids *Prepona* and *Agrias* (Schwanwitsch, 1930, figs. 24, 25, 66, 87), *Charaxes* (Schwanwitsch, 1926, p. 500), *Apatura, Chlorippe* and some others.

§ 4. THIBETANA AND ROXANDRA PATTERNS.

By the preceding section we have ended the consideration of separate components in *Pararge* and now before to pass on to the upperside of the genus we have to deal with its two species taking their underside patterns in the whole.

The underside of *Pararge thibetana* (fig. 35) is rather of peculiar character but the most important modifications observed in it are already referred to. We have seen the melanargoid modifications in its forewing Mediae (ladder-like M^1 dislocation and the M^2 approximation to discal veins in fig. 28), the fragmentation of its hindwing Medial band into $M^1 + M^2$, $M^1 + M^2(4.5)$ and a long posterior part (fig. 35), and the division of its forewing D^2 into two halves (fig. 28). In the distal area of the wings the fragmentation of E^3 has been dealt with (p. 152) connected with the broadening of the stripe in the hindwing (ibid.) and the fusion has been shown (p. 151) of two first Externae into $E^1 + E^2$ (fig. 35) with the subsequent atrophy of the latter (fig. 28). We have now to consider some pecularities in the Umbra of *thibetana*.

In the apex of the forewing the simplest condition shows *thibetana* represented in fig. 35. The anterior end of its Umbra has undergone a bifurcation, very common in this component, and the distal and proximal branches of the latter are designated *Ud* and *Up* respectively. The general character of the two is more or less the same, only *Up* is two or three times as broad as *Ud*. Different is the case of another *thibetana* specimen (fig. 28). Its *Up* does not essentially differ from that in fig. 35, but *Ud* shows a different condition. It has undergone a fragmentation resembling that of E^3. The fragments lying in the 6th and 7th cells are broad and thus their derivation from *Ud* of fig. 35 is obvious. But in the 4th and 5th cells the components designated *Ud* represent small stripes, fairly narrow and convex. They resemble more an Externa than an Umbral derivative. Because, moreover, the component in question is the third from the termen, the idea may be get that the homologisation $E^1 + E^2, E^3$, *Ud* given in the figure of the three stripes running along the termen is inadequate and should be replaced by E^1, E^2, E^3, thus supposing that no fusion of E^1 with E^2 takes place in *thibetana*, and that the component designated *Ud* really represents E^3. But a comparison with *episcopalis* and *praecusta* (figs. 34, 31) shows that such view is hardly tenable. In the 5th forewing cell of the former distally from the eye-spot passes a narrow line *C*. It evidently represents a homologue of the prototypical Circuli and has formed from the Umbra which is broad and dark in other cells of the same specimen (*U*). On comparing the 5th cell of fig. 34 with that of fig. 35 it becomes clear that *C* of the former and *Ud* of the latter are homologous. First both indicated components are the nearest to their respective eye-spots, second the interspaces between the components in question and the eye-spots thelmselves are of a hue which is darker than all more distal interspaces in the same specimens. It should be remarked here that the yellow coloration of the interspaces between the Umbra, or its derivatives, and the eye-spots is very frequent in Nymphaloid families. Now the fact should be emphasized that there are three stripes distal to *C*

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in fig. 34 and only two distal to *Ud* in fig. 35. Because the fusion of the first and second Externae into $E^1 + E^2$ is very common, there is no reason to derive *thibetana* pattern from *episcopalis* in any other way. But if so the stripe designated E^3 in fig. 35 is a genuine third Externa, the fragments $E^3 4$, $E^3 6$, $E^3 7$ in fig. 28 really derive from that Externa, and consequently the two narrow and two broad markings in the 4th to 7th cells of the same specimen are unquestionable fragments of the Umbra. The above consideration could be based on *praeusta* (fig. 31) as well as on *episcopalis* as both forms show considerable resemblance in their apical patterns.

In the posterior cells of *thibetana* a very common process of fusion of the third Externa with the Umbra takes place. In fig. 28 the broad marking proximal to $E^3 3$ undoubtedly represents a part of the Umbra. In the 2nd cell of the same specimen the homologues of the two indicated components are still separate in the anterior part of the cell but their hind ends have fused already. In the 2nd cell in fig. 35 the said fusion is total and an $E^3 + U2$ is the result. The last named component is also connected with the 1st cell portion of M^1.

Now before to pass on to the general characteristics of *thibetana* pattern I have to note some facts which cannot be quite elucidated owing to the fact that *thibetana* stands considerably apart from the bulk of other *Pararge* patterns and no corresponding connecting links are at my disposal. One of them takes place on the forewing. In its discal cell (fig. 28) a broad longitudinal stripe runs along the median vein from the basal corner of the cell to the posterior half of D^2 and the proximally curved hind end of M^2 both said components being fused with the stripe in question. It is not very likely that this stripe derives either from M^2 or from D^2. I think that its derivation is extra-prototypical i.e. it originates from none of the components of the prototype. Most likely it represents a local melanisation of the background similar to that described by me in the posterior cells of some *Melanargia* species (1931, p. figs. 118, 122). Another fact is the presence of a longitudinally stretched marking in the 1st cell of the hindwing which in fig. 32 lies just posteriorly to D^2. It either represents a post-discal prolongation of the last named component, and if so SÜFFERT's scheme of the wing-pattern (1927) in which such prolongation is existing, is more adequate than the prototype in which it is absent (cf. p. 53 in my paper of 1929 a). Or it is a far dislocated 1st cell portion of Basalis, and if so the prototype does not require any alterations. Unfortunately there are no data at my disposal which would allow me to solve this little problem.

As to the general characteristics of *thibetana* pattern the fact should be emphasized that the pattern stands somewhat apart not only from the other species of *Pararge* but also from the common type of Satyrids. There are two main features in *thibetana* pattern particularly in its hindwing which are

meant by this. One of them is the already described fragmentation. We have seen that the third Externa, the coalesced Mediae and the second Discalis have dissolved into fragments which are mostly cellular. Another feature may be called homomorphism. I mean by this that all the mentioned fragments and also the eye-spots look very similar in their coloration, average size and general character. Because the enumerated components are of widely different homologies the acquisition of a similar appearance in all of them deserves attention. The homomorphic fragmentation makes *thibetana* widely different from the common Satyrid type with its generally narrow, mostly uninterrupted stripes.

To complete the description of the underside of *Pararge* we have to examine three specimens of *P. clymene roxandra*. The first of them (fig. 54) shows a number of components. Some of them are well developed as e.g. E^3 and M^1 on the hindwing, some others are degenerating as e.g. the same two stripes on the forewing, but in general the homologies of all the components present are so clear that no further comment is necessary. It should be noted only that the interspace between U and M^1 on the hindwing is white and rather pronounced. In the next *roxandra* specimen (fig. 55) the general degeneration of pattern has considerably advanced, all the stripes have become fainter. The interspace between U and M^1 on the hindwing has almost disappeared owing to a close approximation of the former component to the latter. But in the 4th cell the interspace remains nearly unaltered ($U : M^1 4$) both in its size and coloration. Its preservation is undoubtedly dependent, though not entirely, upon the basipetal dislocation of the hind end of the 4th M^1 cell-portion which has been described in the foregoing as coenonymphoid dislocation (p. 159, figs. 20—27). Finally in the third *roxandra* (fig. 56) no clear remnants of prototypical components are left but several eye-spots and a shortened forewing M^1. The white marking $U : M^1 4$ is however well pronounced in spite of the fact that the first Media which borders it in fig. 55 may be said absent in fig. 56, or in any case having lost the condition of a typical stripe. The condition resulted corresponds to some *Coenonympha* patterns dealt with in chapter XIII and thus the underside of *roxandra* may be described as coenonymphoid pattern in *Pararge*.

CHAPTER III.

UPPERSIDE PATTERNS IN PARARGE.

As I have pointed out in my previous publications (1929 a, 1931) the analysis of the upperside pattern is possible after having established homologies of the corresponding underside. But of course an immediate derivation of

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a highly specialized upperside from a more prototypical form by comparing the uppersides only may be also a good method of research, which will be used in the subsequent description.

With regard to the upperside pattern *Pararge* is a very typical Satyrid with its very conspicuous eye-spots and strong tendency to melanisation (cf. pl. II). This main direction shows however some interesting divergencies in its development, and there are some other directions besides. We have now to consider them.

§ 1. MEGERA TYPE.

The wing-pattern of *Pararge megera* belongs generally to the most prototypical ones. The hindwing of the underside (fig. 36) is quite diagrammatic in both the great number of components present and their condition. If some of them are modified as e.g. bracket-shaped E^2 and E^3, or additional circles in the eye-spots the modifications do not alter considerably the general prototypical habitus. The forewing looks less prototypical owing principally to the oblique course of M^1 and the modified condition of the ocellar series, i.e. elimination of posterior eye-spots and expansion of the 5th one. But in general it is also very prototypical.

It is easy to derive the upperside of *megera* (fig. 37) from its underside (fig. 36). In the forewing the differences between the two are so slight that any comment seems unnecessary. Greater are the distinctions in the hindwing. The most important of them are the following: the first and second Externae have almost fused together into $E^1 + E^2$, and the course of E^2 and E^3 has become less denticulated; a wide interspace $U : M^1$ is present between U and M^1 which is not the case on the underside as its U and M^1 are in contact owing to a greater breadth of the former; M^2 and D^2 have disappeared while D^1 has appeared. The enumerated differences are however not great, and in general the upperside of *megera* may be called prototypical.

§ 2. EGERIA TYPE.

We have now to consider the upperside of *Pararge egeria*. In its highest forms (fig. 41) it deviates greatly from the prototype and its derivation is rather complicate.

The upperside of *egeria* specimen represented in fig. 38 differs considerably in its general aspect from the already examined *megera* specimen (fig. 37) but the homologous relation of the two is rather close. Beginning with the forewing the lack of the first and second Externae should be noted in *egeria* which is however not important as in the next *egeria* specimen both of them are present (E^1, E^2 in fig. 39). The third Externa (E^3) in fig. 38 turns atten-

tion by its marked dislocation in the 3rd cell, where also a considerable portion of the Umbra has fused with the stripe thus forming $E^3 + U$. The first Media (M^1) differs from that of *megera* principally in its basifugal protrusion along the 4th vein which is fused with U. Also a nearly rectangular bending of M^1 should be noted which is due both to the basipetal dislocation of the 3rd cell-portion of the stripe and basifugal one of the 2nd cell-portion. The second Media has undergone a marked pierellisation so that $M^2$1 is much nearer to D^2 than to $M^2$4. But the connection of the two halves of M^2 is still evident. Finally both Discalia (D^1, D^2) and the area of basifugal melanisation (Bm) are well developed in *egeria* forewing, the last named darkening of the ground being initiated also in *megera*.

The most peculiar feature of *egeria* hindwing is that the interspace between the Umbra and first Media ($U : M^1$) is existing only in the 4th and more anterior cells. In the 3rd and more posterior cells the area between U and the wing basis is melanised, so that neither M^1 nor $U : M^1$ are visible there. The correctness of this homologisation is supported first by an immediate comparison with *megera*, secondly by the fact that in some *egeria* specimens which are not figured in my plates I have seen tiny remnants of both M^1 and $U : M^1$ just where they are absent in fig. 38. Besides this the melanisation of the zone between E^3 and the termen should be noted which is curiously restricted to the anterior cells of the hindwing while e.g. in the 2nd cell all the three Externae are visible.

The above consideration shows that *egeria* upperside represents a natural derivative from *megera* pattern and consequently from the prototype. Further evolution of *egeria* pattern to be traced now principally consists in the expansion and small dislocations of the components present and in an orderly melanisation of some of the interspaces. Let us consider first the origin of the female *egeria* pattern represented in fig. 40. With regard to the process in question the interspaces of the forewing present in fig. 38 may be classified under two categories. Some of them tend to persist, othere are liable to suppression. Those belonging to the first category are all distal to the first Media, those proximal to the indicated stripe belong to the second one. Beginning with the first category it should be pointed out that in fig. 38 there are three respective interspaces: one rather narrow between E^3 (or $E^3 + U$) and the termen, another restricted to the anterior cells designated $E^3 : U$ according to its confining components, still another designated $U : M^1$ in the anterior cells and $E^3 : M^1$ in the posterior ones. This latter interspace is already subdivided into parts corresponding to the just named indexes, the subdivision being due to the coalescence of M^1 with U on the 4th vein.

In the next *egeria* specimen (fig. 39) the just described interspace is divided into four parts instead of two. The most anterior of them ($U : M^1$) differs from its homologue in fig. 38 only by a smaller size which

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is dependent upon the expansion of both U and M^1. The next part $U : M^1 3$ has become narrower than its homologue in fig. 38 owing to the expansion of $E^3 + U$ and has separated from the third part designated $E^3 : M^1 2$ that being dependent both upon the said expansion of $E^3 + U$ and the basifugal dislocation of M^1 in the 2nd cell which stripe is now placed exactly on the geometrical prolongation of $U : M^1 3$. The last part $E^3 : M^1 1$ has separated from the preceding one owing to the appearance of a veinous stripe on the 2nd vein.

As to the other interspaces distal to the first Media two of them are noteworthy. The anterior one $U : U$ originates from $E^3 : U$ of fig. 38 by the way of accumulation of the "Umbral substance" along E^3. The distal one $E^2 : E^3 3$ represents a small remnant of the long terminal area of fig. 38 in which E^2 has appeared, and a wide melanisation developed.

In the next *egeria* specimen (fig. 40) all the above described interspaces are still more individualised owing to a further advancement of the processes which they have resulted from. A peculiar cross-shaped figure has thus arisen in the terminal zone of *egeria* forewing. The long axis of the cross is represented by $U : U$, $E^3 : M^1 2$ and $E^3 : M^1 1$, the short one is composed of $E^2 : E^3 3$ and $U : M^1 3$. The fact should be emphasized that the three first named interspaces might seem to belong to one series, as their general character and the distances from the termen are nearly the the same in all of them, but their real homologies have been shown to be quite different.

The described position of the interspaces distal to M^1 is the most salient feature of the forewing pattern represented in fig. 40. As to the interspaces proximal to M^1 their gradual disappearence is readily seen. In fig. 38 they are very numerous: $D^1 : M^2 4$, $M^2 4 : D^2$ and $D^2 : Bm 4$ in the discal cell, $M^1 : M^2$ and $M^2 : Bm 1$ in the 1st and 2nd ones. In the next figure those adjacent Bm (i.e. $D^2 : Bm 4$, $M^2 : Bm 1$) have vanished owing to the expansion of Bm, those enclosed between the Mediae (i.e. $D^1 : M^2 4$, $M^1 : M^2$) have darkened (though subdivision of $M^1 : M^2$ into $M^1 : M^2 2$ and $M^1 : M^2 1$ should also be noted) and that between the second Media and second Discalis ($M^2 4 : D^2$) shows no alteration in color. In the final specimen (fig. 40) the last named interspace ($M^2 4 : D^2$) is still retined though being very narrow, while all the other interspaces in question have so darkened that they do not play any important rôle in the general appearance of the pattern, the latter being principally dependent upon the peculiarly placed interspaces distal to the first Media which are already described.

By this the analysis of the forewing of *egeria* female is completed. The evolution of the hindwing is simpler. It has been shown in the foregoing derivation of *egeria* pattern from that of *megera* that the posterior part of the Umbro-Medial interspace $U : M^1$ disappears owing to melanisation (p. 166). The rest of the interspace restricted to the anterior cells beginning

with the 4th one undergoes but small alterations in the subsequent evolution, viz. in the 5th and 6th cell the Umbra slightly advances basipetally and adheres M^1, though without actual fusion. This is the case in both figs. 39, 40. The Umbro-External interspace ($E^3 : U$) in which the eye-spots lie is very wide in fig. 38, has narrowed in fig. 39 and still more so in fig. 40. No change in the confining components seems to accompany the narrowing with the exception of the 2nd cell in fig. 40 where the exactly concentric shaper of the interspace (iU) and its eye-spot suggest the idea that most likely the total circumference of the interspace is built of the Umbral elements thus supposing the latter to have accumulated on E^3 (which stripe is so well pronounced e.g. in the 2nd cell in fig. 38) and replaced this stripe in confining the light circum-ocellar zone. That being so the yellow ring surrounding the eye-spot in the 2nd cell in fig. 40 should not be called Umbro-External but rather intra-Umbral. Such intra-Umbral circum-Ocellar interspaces are very common and may be seen in almost every of the figures 41—51. The chief argument favouring the homologisation given is that the third Externa when present is mostly inclined to manifest its independent nature and to acquire every form but that concentric to the eye-spots. On the contrary the Umbra is a typically passive component, and the cases of its being exactly concentric to the eye-spots are extremely abundant. Hence if in the place of an interspace limited by an undoubted E^3 appears one exactly concentric to the eye-spots it is much more plausible to admit the intruison of some new Umbral elements covering the proximal side of third Externa than an alteration in the typical properties of the last named stripe. The exceptions from this rule are unfrequent, one of the cases of such abnormally passive behaviour of E^3 is recorded by me in the Satyrid *Anadebis* (1929 b, p. 44). In the same paper the passive character of the Umbra is discussed (p. 41).

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We have now to examine the upperside of a male of *egeria* v. *xiphioides* which exhibits some deviations from the above described pattern. It is readily seen that in fig. 41 the interspaces $D^1 : M^2 4$, $M^2 4 : D^2$, $D^2 : Bm4$, $M^1 : M^2 2$, $M^1 : M^2 1$ and $M^2 : Bm1$ are present which in the preceding figure are either very narrow ($M^2 4 : D^2$) or do not exist as light markings owing to their strong melanisation. The homologues of all of them may be, however, easily seen in fig. 39 and still better in fig. 38. Particular attention deserve the considerable width of $M^2 4 : D^2$ surpassing that of preceding *egeria* specimens, and the narrowing of $M^1 : M^2 2$ and $M^1 : M^2 1$ due to a marked broadening of M^2 in the 1st and 2nd cells. The last named fact is dependent upon the presence of androconia on the distal border of M^2.

As to the rest of *xiphioides* upperside only one difference should be noted on the forewing, viz. the absence of the interspace $E^2 : E^3 3$ so typical of the

preceding specimen; meanwhile the deviations of the hindwing from fig. 40 are so minute that any further explanation is unnecessary.

Thus we have analysed two highly specialised uppersides (figs. 40, 41) occuring among *egeria* forms. Their immediate comparison to the prototype would scarcely lead to a correct homologisation but the evolutionary series as described in the foregoing shows most clearly how the dislocations and broadening of stripes and darkening of interspaces result in patterns which give impression of light markings irregularly distributed on dark background. The analysis given proves, however, that the distribution is orderly and that every marking depends in its position, size and form on those of the confining prototypical components. Finally the fact should be emphasized that nigrism, i.e., broadening of pattern components plays nearly as important rôle in *egeria* upperside as melanisation, i.e., darkening of the interspaces. Generally, however, nigrism is not frequent in Satyridae and undoubtedly the somewhat aberrant habitus of *egeria* compared with common Satyrid type is due to its nigrism.

§ 3. MELANISED PATTERNS.

In the present paragraph several uppersides will be dealt with which are of a more typical Satyrid character as their development consists principally in melanisation.

In fig. 42 the upperside of *Pararge megera* is represented which differs from the previously described one (fig. 37) in a stronger development of the Umbra and of melanisation. On the hindwing the former (U) nearly fills up the interspace between M^1 and E^3 while the eye-spots are surrounded by the intra-Umbral rings (iU) the definition of which is given in the preceding paragraph (p. 168). A marking of this sort containing a tiny eye-spot rudiment is seen in the 5th hindwing cell.[1] Another marked $E^3 : U$ lies distally from it. The two indicated markings owe their origin to the separation of iU from some large $E^3 : U$ interspace like that present in the same cell in fig. 37. The total of the area proximal to M^1 on the hindwing has considerably melanised, the same is the case on the forewing in the basal area, and along the dorsum in the cell posterior to the 1st one. An obvious inclination to darkening in the enumerated places is readily seen in the preceding *megera* (fig. 37) as well.

The upperside of *Pararge sicula* (fig. 43) almost does not differ from fig. 42 in the number of components present. The only important homologous difference is the absence of the first Media on the hindwing which is dependent upon the total melanisation of the area proximal to the eye-spots

[1] The rudiment has almost totally disappeared in the process of the reproduction of plates.

and their Umbral rings (*iU*). On the forewing the distribution of melanisation is different, viz., it is restricted to the whole of the area proximal to the first Media (M^1), while that distal to the said stripe is not more melanised than in the preceding figure. The fact should be emphasized now that melanisation on the forewing being wide is, however, not strong so that all the pattern components located in the melanised area (D^1, M^2, D^2) are visible.

This is not so in *Pararge maera* v. *adrostoides* (fig. 44). In its forewing the wide area between M^1 and the wing basis and the narrow one distal to E^3 are so dark that one cannot discern any components in them. The hindwing differs from that of the preceding specimen also in its complete melanisation of the zone of Externae so that E^3 is the only stripe more or less conspicuous there. Thus the *adrastoides* upperside is melanistic. It is widely differing from that of *megera* but neither dislocations nor broadenings of any components are responsible for the difference. The salient feature of *adrastoides* upperside is the strong melanisation of the total of both wings except for the wide Medio-External area ($E^3 : M^1$) on the forewing and a few intra-Umbral rings (*iU*) on the hindwing. It is interesting to notice here that *adrastoides* has nearly lost its forewing Umbra, only a tiny remnant of which is conspicuous in fig. 44 while a pronounced *U* is lying in the same place in fig 43.

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A still greater extent of melanisation is observed in *Pararge maera*. The forewing (fig. 45) shows nearly the same degree of melanisation as that in fig. 43: E^2, E^3, *U*, M^1, M^2, D^1 are visible though on a fairly dark ground. The difference however is that the area between E^3 and M^1 which is light in fig. 43, has darkened considerably in fig. 45. The darkening cannot be ascribed to an expansion of the Umbra, since the latter remains very well individualized in the area proximal to the large 5th eye-spot. Hence the process should be regarded as a genuine melanisation. Only one area does not undergo it, viz., the intra-Umbral rings. In another *maera* (fig. 46) two of the said rings together with their eye-spots are the only parts of the pattern all the rest being vanished owing to a further melanisation. Similar is the case of the hindwing in *maera* while in *hiera* M^1 and the Externae are visible yet.

Thus we have traced two directions of melanisation in *Pararge*, which being practically identical on the hindwing are different on the forewing, viz. only small intra-Umbral rings are left not melanised in *maera*, while so is the wide Medio-External interspace in *adrastoides*.

Let us examine now three uppersides showing each some distinctive characters in melanisation.

Pararge dumetorum (fig. 48) is somewhat similar to *egeria* type, as it has typical $U : U$, $U : M^1$ and $M^2 : Bm4$ interspaces on the forewing and a remnant of $U : M^1$ on the hindwing. But firstly $U : M^1$ on the forewing has

not dissolved into cell fragments so typical of *egeria*, secondly there are no interspaces between the forewing Mediae.

The forewing of *Pararge deidamia* (fig. 49) resembles *adrastoides* (fig. 44) in its total melanisation of the area proximal to M^1. But the former exhibits a pronounced Umbra (U) which even subdivides the $U : M^1$ interspace, while in the latter the Umbra is almost absent. The forewing of another *deidamia* (fig. 50) exhibits essentially the same pattern but $U : M^1$ has undergone a marked darkening which has caused a considerable difference in the habitus of the two *deidamia* specimens. The relation of their hindwings has to be noticed. In fig. 50 $U : M^1$ is still conspicuous, in fig. 49 they are absent owing to a stronger melanisation. Externae are visible in both specimens.

The last melanised *Pararge* upperside to be dealt with is that of *episcopalis*. We have seen (p. 160) that on its forewing underside (fig. 34) the first Media (M^1) acquires a pronounced oblique direction. The corresponding Umbra (U) is not wide but sufficiently pronounced, so that the homologisation of the white $U : M^1$ interspace requires no further comment. On the upperside (fig. 33) $U : M^1$ is reproduced fairly exactly though being narrower. The rest of both wings is melanised almost totally, the only other parts left are the 5th eye-spot and the 6th ocellar marking on the forewing and the narrow interspace $E^2 : E^3$ on the hind one. Thus the forewing $U : M^1$ crossing obliquely the dark whole of the wings represents the sole part of the upperside pattern important with regard to the habitus. This sort of pattern stands somewhat apart from the bulk of palaearctic species dealt with in the present investigation, and reminds more Southern forms like e.g. *Lethe* or even typical exotic genera of other Nymphaloid families as e.g. *Catagramma*, *Callicore* and others in which such oblique bands are common.

§ 4. ELIMINATION ON THE UPPERSIDE.

After having studied several examples of nigrism and melanisation in *Pararge* we have to deal with an opposite tendency. Its beginning may be seen in *Pararge maera* v. *menava* (fig. 51). Generally *menava* upperside differs but slightly from that of *sicula* (fig. 43). The latter, however, exhibits well pronounced uninterrupted Externae, the third one (E^3) being particularly heavy. Just the opposite is the case on the forewing of *menava*. Its E^3 shows marked atrophy being narrow, faint and even interrupted on the veins. E^2 and U may be described as atrophying in *menava*.

The tendency of elimination of components is much stronger in *Pararge eversmanni*. Its underside (fig. 53) is rather prototypical except for the already described coenonymphoid dislocation in the hindwing M^1 and the elimination of the posterior ends of Mediae of the forewing. On the upperside (fig. 52) only a few of the numerous underside components are present.

There are several unpupillated eye-spots on both wings, first Discalis (D^1) and a small remnant of the Umbra (U) on the forewing, and a dark rim running along the termen of both wings. As comparison to the underside shows the melanisation of the narrow area between the third Externa and the termen is responsible for the greater part of the rim. But the Umbra also takes a part in it where the rim forms outgrowths, viz. in the anterior cells of the hindwing and in the third cell of the forewing (U_3). Also the broadening near the apex of the forewing is evidently due to the Umbra. All the other components, however, have totally vanished from the *eversmanni* upperside. Their faint traces seen in fig. 52 are the underside components visible through the wing. Both the described elimination of the great part of components and the very restricted scale of melanisation are two salient pecularities of the pattern in question in which it differs from other forms of its own genus and from the common Satyrid type. But they are not unparallelled as *Satyrus huebneri* v. *dissoluta* STGR. described in the first part of the present investigation shows very similar upperside in which the principal parts are a few eye-spots, terminal brim limited by E^3 and a complex marking on the discal veins of the forewing (1929 a, p. 625, figs. 153, 154). There are some distinctions between the two patterns but the general tendency is undoubtedly the same in both.

Thus we see that the upperside patterns of *Pararge* display rather a considerable variety, though some of them, as e.g. that of *Pararge achine*, are intentionally left out of consideration as not very interesting morphologically. We will return to *Pararge* upperside when discussing the Oudemans' phenomenon as observed in the genera dealt with in this paper.

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CHAPTER IV.

REALISATION OF THE NYMPHALOID PROTOTYPE IN THE GENUS EPINEPHELE.

According to SEITZ the genus *Epinephele* HBN. consists of 21 species and 81 forms. Whith regard to the wing-pattern it is one of the most typical genera of palaearctic Satyridae, being very modest in coloration and showing prototypical components in very clear forms. Let us see now how the prototype is realised in the genus.

In *Epinephele amardaea* (fig. 58) three Externae (E^1, E^2, E^3) and two Mediae (M^1, M^2) are well pronounced on both wings. There are also two eye-spots, the Umbra (U) rather typical on the hindwing is represented by a part of Circulus (C) on the fore one. The pattern formula of *amardaea* is:

$$\frac{E^1.\,E^2.\,E^3.\,OC\,(-\!-\!-\!-\!-\,5.\,-\!-\!-\!-)\;U.\,M^1.\,M^2.\,-\!-\!-\!-\!-\!-\!-\,|\,-\!-}{E^1.\,E^2.\,E^3.\,OC\,(-\,2.\,-\!-\!-\!-\!-\!-\!-)\quad U.\,M^1.\,M^2.\,-\!-\!-\!-\!-\!-\!-\,|\,-\!-}$$

Thus 14 components are present in it and 27 absent. Some of the components absent in *amardaea* exist, however, in other *Epinephele* forms. The ocellar formula of *Epinephele pasiphaë* (fig. 59) is $\frac{OC(-\!-\,3.\,4.\,5.\,-\!-\!-\!-)}{OC(\,1.\,2.\,3.-\,5.\,6.-)}$. The 4th and 5th forewing eye-spots fused in *pasiphaë* are separate on the upperside of *rückbeili* (fig. 61). On the underside of the same specimen (fig. 65) a small *OC6* is existing, in *lycaon* (fig. 66) a pronounced *OC2* is present. On the hindwing of *rückbeili* (fig. 67) the 4th eye-spot is well developed which has vanished from *pasiphaë* series. On summing up all the indicated eye-spots the following generic ocellar formula is obtained:

$$\frac{OC(-\,2.\,3.\,4.\,5.\,6.-\!-).}{OC(\,1.\,2.\,3.\,4.\,5.\,6.-).}$$

It is much more complete than that of *amardaea*.

The same *pasiphaë* specimen (fig. 59) exhibits a very typical Umbra (*U*) on the hindwing and a rather pronounced one on the forewing. The forewing first Discalis (D^1) is seen in another *pasiphaë* (fig. 62), that of the hindwing in fig. 68. Besides this a rather rectilinear course of E^3 should be noted in figs. 60, 64 instead of denticulated one in our initial specimen. The presence of M^2 in the 1st cell in fig. 63 and its undisturbed condition in the discal cell in fig. 68 also represent more prototypical status than that observed in *amardaea*.

If adding now to the above *amardaea* formula the already obtained formula of eye-spots and the indexes of the first Discalia of both wings we get the generic formula of *Epinephele* as follows:

$$\frac{E^1.\,E^2.\,E^3.\,OC\,(-\,2.\,3.\,4.\,5.\,6.-\!-)\;U.\,M^1.\,M^2.\,-\!-\,D^1.\,-\!-\,|\,-\!-}{E^1.\,E^2.\,E^3.\,OC\,(\,1.\,2.\,3.\,4.\,5.\,6.-)\quad U.\,M^1.\,M^2.\,-\!-\,D^1.\,-\!-\,|\,-\!-}$$

It contains 25 members thus only 16 out of 41 components of the prototype being absent in it. It is obvious that the latter is realised in *Epinephele* fairly completely, and the diagram of hypothetical *Protepinephele* (fig. 57) built up on the basis of the above formula better illustrates the connection of the genus with the prototype than a wordy explanation. As to the lacking components the absence of the second Discalia and Basalia is especially important as these components are absent in all the palaearctic genera dealt with in the present investigation except for *Pararge*.

CHAPTER V.

MODIFICATIONS OF THE WING-PATTERN ON THE UNDERSIDE OF EPINEPHELE.

Let us consider now which are the principal modifications which the components of the prototype undergo in *Epinephele* and begin with those on the underside.

§ 1. EXTERNAE.

The most common modifications observed in the Externae are the elimination of the second Externa and the acquisition of different shapes in the cell portions of the third one.

In *Epinephele amardaea* (fig. 58) we have seen a fine second Externa (E^2). On the forewing of *E. narica* (fig. 71) the same stripe shows a marked atrophy, which has so advanced in the hindwing of another *narica* (fig. 75) that the stripe is quite vestigial. The total disappearance of E^2 may be seen in many *Epinephele* as e.g. figs. 70, 74, 83 and others. Exactly the same process is described by me in *Satyrus* (1929 a, p. 571) and in *Melanargia* (1931, p. 326). In *Pararge* the second Externa has been shown to disappear by fusion with the first one (p. 151). There are no data at my disposal proving the fusion in *Epinephele* but e.g. the participation of E^2 in rather broad stripes designated as E^1 on the hindwings of *E. davendra* and *wagneri* (figs. 102, 104) is not absolutely unlikely.

The prototypical form of the cell-portions of third Externa is rectilinear, which status is approached in figs. 60, 64, 66. In *amardaea* and *pasiphaë* (figs. 58, 69), however, E^3 forms typical concave crescents in every cell. The opposite modification i.e. convex E^3 cell-portions is well pronounced in *Epinephele pulchra* (fig. 70) and *E. hilaris* (fig. 74). The former modification is very typical of *Melanargia* (1931, p. 328), the latter of *Satyrus* (1929 a, p. 573). The third modification is observed in *Epinephele narica* (figs. 71, 75) where some E^3 cell-portions consist of two concave crescents each thus being concave bi-arcuate. This modification is reverse to one very typical of *Pararge* in which genus bi-arcuate E^3 cell-portions are convex (fig. 36).

Finally returning again to the second Externa its becoming diffuse on the proximal border should be noted. The beginning of the process is conspicuous on the forewing in fig. 71 and on the hindwing in fig. 58. In both wings of *pasiphaë* (fig. 69) the process is more advanced, and still more so in another *pasiphaë* (fig. 59). In *Satyrus geyeri* similar modification has been recorded by me (1929 a, p. 571, fig. 20).

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§ 2. EYE-SPOTS.

There are several modifications in eye-spots to be considered in this paragraph.

A. Ereboid dislocation.

The first of them is the ereboid dislocation i.e. basipetal shifting of the 4th and 5th eye-spots on the forewing (cf. p. 155). In *Epinephele tithonus* (fig. 72) the indicated dislocation is but slightly developed particularly in the 4th cell. In *E. pasiphaë* (fig. 73) not only the 5th but also the 4th eye-spots are markedly displaced basipetally. That becomes quite clear when comparing them to 3rd and rudimentary 6th ones which are undislocated. An imaginary line connecting the latter with each other would be parallel with the termen, while almost the whole of coalesced 4th and 5th eye-spots would be placed proximally to that line. The modification has been recorded already in *Pararge* (p. 155) and *Satyrus* (1929 a, p. 580).

Like *Pararge* erebisation takes place also on the hindwing. In *Epinephele tithonus* (fig. 100) the eye-spots are replaced by white ocellar markings. That in the 3rd cell lies close by the third Externa while that in the 5th one is situated nearer to M^1 than to E^3 being thus dislocated basipetally. There is no trace of any ocellar component in the 4th cell. Its most likely position, if present, would be on the level between the 3rd and 5th ocellar markings. But at any rate the indicated position of the 5th marking suffices to assume the existence of erebisation on the hindwing of *tithonus*.

B. Positional inversion.

The significance of the modification to be dealt with in the present section could be hardly estimated without my previous research on the South American Nymphalid genus *Prepona* (1930 b). In the indicated paper the notion of positional inversion of pattern components is formulated. One of the forms of inversion (see text-fig. 3) is that the third Externa (E^3) on the hindwing dislocates basipetally, the eye-spots which are either stationary or move a little in the opposite direction, pierce the advancing stripe as it were, and the latter comes to lie proximally to the ocellar series, thus the two components of the prototype acquiring inverted positions.

There is no doubt that in *Epinephele dysdora* we have first stages of this remarkable process. In fig. 76 the 1st and 2nd eye-spots ($OC1$, $OC2$) lie proximally to the faint third Externa fused with the Umbra ($E^3 + U$), but the 1st eye-spot ($OC1$) has closely approximated to the distal boundary of the stripe. In another *dysdora* (fig. 77) $E^3 + U$ is better pronounced and it

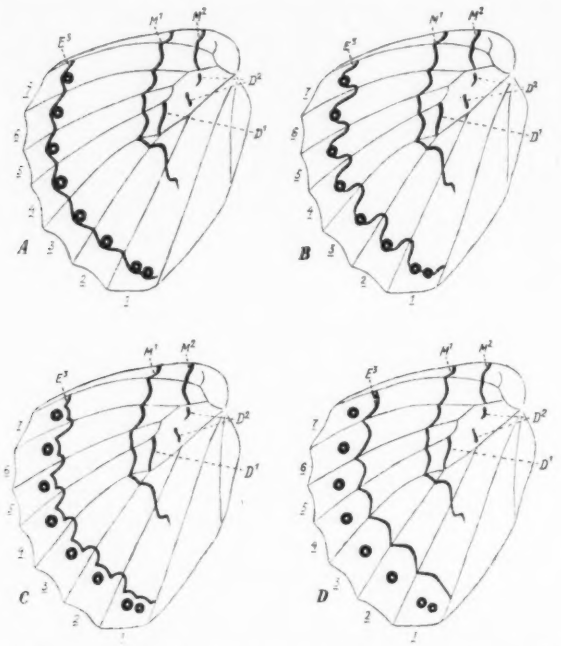

Fig. 3. Diagram of the positional inversion of the third Externa (E^3) and eye-spots in *Prepona*. A. E^3 is distal to eye-spots as in the prototype (text-fig. 2, p. 147). B. E^3 is dislocated basipetally on the veins, the eye-spots pass through it. C. E^3 has broken off from the eye-spots and is proximal to them, its shape shows the traces of vanished contact. D. E^3 has acquired its normal chape, the inversion is completed. For lettering see text-fig. 2, p. 147. (SCHWANWITSCH, 1930.)

is readily seen that $OC1$ has pierced the stripe $E^3 + U$, and partly entered the light interspace $E^1 : E^3$. The described relations may be made still clearer as follows. In fig. 76 the light ring round $OC1$ is continuous, and the area $E^1 : E^3$ is separated from it by a tiny line of $E^3 + U$. The latter has vanished from fig 77, the light ring is widely interrupted owing to its fusion with $E^1 : E^3$ and has become horseshoe-shaped. Therefore there is no component separating $OC1$ from $E^1 : E^3$, the distal end of the former is practically lying in the latter, or in other words the 1st eye-spot has crossed over the third Externa. Supposing the process to advance further the eye-spot could become totally distal to E^3, and thus complete inversion would be resulted in like that described in *Prepona*.

On the other hand the above condition reminds that described by me in *Melanargia* (1931, p. 354). The 2nd eye-spot ($OC2$) in *Epinephele dysdora* lies rather far from E^3 and as a comparison to fig. 69 suggests this is a result of the general condition of the ocellar series, viz. of the fact that the posterior eye-spots lie nearer to E^3 than the middle ones. Similar condition in *Melanargia* leads to a partial crossing of the 1st cell eye-spots over the third

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Externa. The result is however differing from that in *Epinephele* viz. in *Melanargia* either the crossover parts disappear of both E^3 and the eye-spots, or only those of the latter undergo disappearance. Just the opposite is the case in *Epinephele* where only a small particle of E^3 seems to be lost, as if being covered by the eye-spot while the latter remains unaltered. Thus the same cause i.e. the contact of the third Externa and the eye-spots has different consequences in the two genera. The fact should be emphasized here that the tendency of positional inversion which is perhaps the most powerful of the factors governing the evolution of the wing-pattern manifests itself not only in the highest groups of Nymphaloid families like that of *Prepona* and *Agrias* but in a restricted scale does so in such comparatively primitive genus as *Epinephele* is.

C. Elongation of the 5th eye-spot on the forewing.

The modification to be dealt with now takes place on the upperside only. Its development looks very simple. In *Epinephele davendra* (fig. 78) the 5th eye-spot ($OC5$) on the forewing shows normal circular form. In *E. wagneri* (fig. 79) it is elongated, in another *wagneri* (fig. 80) it represents a rather long oval, and in a still another *wagneri* (fig. 81) its length nearly trebles its breadth. Thus the 5th eye-spot undergoes a very strong expansion which is, however, restricted to only one direction namely to longitudinal one, as even in fig. 81 the eye-spot does not cross over the confining veins. On the other hand it is very interesting that on the underside $OC5$ is not inclined to elongate at all, as it is seen in fig. 82 which is made from the underside of the same specimen as fig. 81, thus an uncommon independence of the two surfaces of the wing being the case. A comparison of the two surfaces with each other shows that during the above process the unmodified underside $OC5$ remains on the level with the distal end of the elongated upperside $OC5$. Thus evidently the eye-spot elongates in basipetal direction only.

Finally the elongating eye-spot influences the adjacent first Media (M^1) in a way described by me as pressure (1926, p. 504) and by KÜHN as repulsion (1926). In figs. 78—80 the shape of M^1 does not show any dependence upon that of $OC5$. In fig. 81 M^1 is markedly curved in on the level of $OC5$, the curvation being exactly concentric with the circumference of the latter. The impression born out is that $OC5$ presses upon M^1 though there is an interspace between the two. Quite similar examples of activity of eye-spots are described in details in one of my previous publications (1929 b, p. 41).

It is noteworthy that on the underside M^1 remains unaltered so that if looking through the wing of the specimen represented in figs. 81, 82 it is readily seen that the proximal end of upperside $OC5$ crosses over the 5th cell-portion of underside M^1.

D. Combinations.

The hindwing of *Epinephele* is sometimes multiocellate (figs. 59, 67) though often the 2nd eye-spot is the only present (fig. 58), or even none is left (fig. 98). On the forewing multiocellate condition is less frequent (figs. 61, 72) but even in such forms the 2nd, 4th and 5th eye-spots are the largest, which generally represent the most stable components in the ocellar series. In the forewing the combinations $OC(---2.---5.----)$ seen in fig 96, $OC(-----5.----)$ in fig. 98 and $OC(----4.5.----)$ in fig. 100 seem the most typical of *Epinephele*. If considering both wings together the formulae $\frac{OC(-----5.----)}{OC(---2.-------)}$ in fig. 58, $\frac{OC(---2.---5.----)}{OC(---2.-------)}$ in fig. 96 and $\frac{OC(-----5.----)}{OC(---------)}$ in fig. 98 may be regarded as the most characteristic. All the above ocellar combinations do not deviate from those occurring in some other Satyrid genera under investigation.

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§ 3. MEDIAE.

Let us now pass on to a few modifications in the Mediae of *Epinephele*. The first to be dealt with is the oblique position of the first Media (M^1) on the forewing. Its gradual development is seen in the series of four specimens beginning with *davendra* (fig. 83) in which M^1 is nearly parallel to the termen and ending with a *janiroides* (fig. 86) in which M^1 and the termen form an angle. Two specimens of *wagneri* (figs. 84, 85) exhibit transitionary conditions. The obliquity reached is not very considerable being just of the degree reached in *Pararge* (fig. 19), *Satyrus* (1929 a, fig. 55) and *Melanargia* (1931, fig. 11).

On the hindwing the first Media undergoes a peculiar curvation. In *Epinephele dysdora* (fig. 87) M^1 is rather prototypical, in the next *dysdora* (fig. 88) it is somewhat bent down, in *wagneri* (fig. 89) it has become rather regularly curved, and in another *wagneri* the curvature has strongly increased towards the hind end of the stripe (fig. 90); near the 1st vein, however, M^1 turns its direction and forms a small hook. The general form of the stripe resulted in is very singular, and there is no parallel at my disposal now to this modification in other genera.

The last modification to be considered in M^1 is the appearance of yellow coloration in the middle part of the stripe on the forewing. The most typical status is seen in fig. 86 where only the anterior and posterior ends of M^1 are of normal brown color while all the rest is ochreous yellow. In fig. 85 the total of M^1 is brown, in fig. 83 the total is yellow, thus fig. 86 representing a transitionary condition between the two last named figures. The process

develops exactly along the lines described by me in *Satyrus* (1929 a, p. 593) in which genus it is followed by the elimination of the yellow parts of stripe. The same tendency is seen in *Epinephele davendra* (fig. 102) and *E. tithonus* (fig. 100).

As to the second Media some inclination to pierellisation (cf. p. 157) is conspicuous in fig. 63 where the discal portion of M^2 is approximated to the discal veins, while the hind end of the said portion has dislocated basipetally. The proximally directed denticle in the hindwing M^2 in fig. 58 may be regarded as "triphysoid" modification similar to that described by me in *Satyrus* (1929 a, p. 600). Another modification reminding *Satyrus* is the elimination of M^2 from both wings. The beginning of the process is seen in figs. 96, 102 where M^2 still persists on the hindwing. The completion of it is well pronounced in figs. 94, 98, 104 in which M^2 is totally absent, while M^1 remains strong enough. The conditions resulted in resemble closely that described by me in *Satyrus parisatis* (1929 a, p. 605). But the process may go further. *Epinephele lycaon* v. *intermedia* (fig. 91) corresponds to the just described status, but from another *intermedia* (fig. 92) M^1 has also vanished thus the forewing E^3 and a single eye-spot being the only parts of the pattern.

CHAPTER VI.

UPPERSIDE PATTERNS IN EPINEPHELE.

The upperside patterns in *Epinephele* are less complicated than in *Pararge* and their comparatively restricted diversity is principally dependent upon the differences in the distribution of melanised areas.

The upperside of *Epinephele pasiphaë* (fig. 93), as a comparison to its underside (fig. 94) shows, represents a rather pure form of Medio-External pattern. There are two large areas of melanisation in it, one distal to E^3, another proximal to M^1. The large interspace between the indicated components ($E^3 : M^1$) remains quite unmelanised; the Umbra well pronounced below (U in fig. 94) does not penetrate on the upperside except in the small areas near the costae of both wings. One more fact is noteworthy. The first Media on the upperside of the hindwing (M^1 in fig. 93) is dislocated basipetally in the middle cells, while on the underside it does not show the indicated dislocation. Owing to the fact that the underside first Media is seen on the upperside through the wing-membrane (M^{1*}) the indicated incongruity is readily observable in fig. 93. Similar interrelations have been recorded by me in *Satyrus hermione* (1929 a, p. 611) with the difference that in it the upperside M^1 is more distally placed than the underside one.

The light area on the forewing of *Epinephele lycaon* ($E^3 : M^1$ in fig. 95) may be also regarded as rather purely Medio-External, though undoubtedly

participation of the Umbra in it is greater than in *pasiphaë*, particularly in its fore and hind ends. The dark streak on the 4th vein and entering by its sharp proximal end the area proximal to M^1 represents either a Venosa or a local melanisation. In *Satyrus anthe* similar streak on the 4th vein has been recorded by me (1929 a, p. 613) which arises, however, in connection with protrusions of M^1 and E^3 towards each other along the indicated vein. In *Epinephele* no such protrusions develop (cf. fig. 96) and thus the crossing over of the $E^1 : M^1$ interspace by a dark streak is reached by other means. On the hindwing E^3 and M^1 are well conspicuous, the interspace between them ($E^3 : M^1$) is strongly darkened. The darkening may be ascribed to the Umbra which is pronounced on the underside, but it is not unlikely that melanisation might be responsible for it. The cases like this demonstrate once more (cf. my paper of 1931, p. 386) that there is some affinity between Umbra and melanisation not sufficiently analysed yet.

One more very interesting circumstance deserves attention. On the forewing upperside of *Epinephele lycaon* (fig. 95) there is a pronounced basifugal melanisation (*Bm*) showing typically diffused margin. The latter is shaped largely concave, and passes from the costal area into discal cell, then turning distally it crosses the 2nd and 1st cells so obliquely that its hind end lies near the tornus. One of the results of the described course of the *Bm* margin is that the light interspace $E^3 : M^1$ and the light area between M^1 and *Bm* evidently represent one large field, the unity of which does not suffer from the fact of its being crossed by M^1. Another result is that the *Bm* margin and the hind end of M^1 cross over each other in the 1st and 2nd cells forming there a sort of x-shaped figure. Owing to the diffused margin of *Bm* and owing to the fact that M^1 emits small basipetal melanisation the exact point of their intersection cannot be indicated though it seems very likely that it is placed in the 1st cell quite near by the 2nd vein. But the very existence of crossing over is doubtless as it follows as an inevitable result from the general positions and directions of the components in question.

In my paper on *Melanargia* I have noticed that the basifugal melanisation tends to spread "quicker" along the dorsum of the wing than in any other direction. This statement is in accordance with the above data about *Epinephele lycaon* melanisation. It should be pointed out, however, that in *Melanargia* the things stand somewhat differently: its different cells mostly differ greatly in the extent of the basifugal melanisation, so that I have not been able to see in it such uninterrupted margin of *Bm* from costa to tornus as it is the case in *Epinephele lycaon*. But in *Pararge egeria* (fig. 38) the margin of *Bm* is continuous and passes from costa to dorsum. It crosses the 1st cell very obliquely and its crossing over the Mediae is avoided only owing to the fact that the area of *Bm* has spread not sufficiently far yet. The resemblance between the areas in question of *Epinephele* and *Pararge* leaves

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no doubt of their homology, and the indicated difference is only quantitative. It is possibly typical of the margin of basifugal melanisation to pass from the costa to dorsum or tornus crossing the border cells at a considerable angle and not being parallel to the termen at all. Because on the contrary all the prototypical transverse stripes are more or less parallel to the termen their crossing over the margin of *Bm* is the result when they meet each other. We have seen it in M^1 of *Epinephele lycaon* and the same is nearly existing in M^2 of *Pararge egeria*.

In my paper on *Pierella* group (1928) the notion of crossing over is formulated, in the paper on *Prepona* and *Agrias* I have numbered it among the examples of a more general phenomenon of the positional inversion of components (1930 b, p. 391). It is difficult to consider the *Epinephele* case as positional inversion since by the latter the process is meant occurring in the components of the prototype, to which the basifugal melanisation does not belong. But if it is not a positional inversion exactly in the above sense it nevertheless resembles so closely the crossing over of the ocellar series and Umbra in *Pierella* that undoubtedly the two cases have much in common.

The upperside of *Epinephele janira* (fig. 97) differs from that of *lycaon* in a further darkening of the hindwing so that E^3 has become scarcely discernible, while M^1 is visible only in the 4th and 5th cells. The light marking in the 4th cell ($U : M^1$) seems to be undoubtedly Umbro-Medial since its distal boundary looks as a typical margin of an Umbra. The confining components of the light area on the forewing are the first Media (M^1) and the third Externa (E^3). Because, however, some Umbral elements have obviously made diffused its distal boundary having joined to E^3 particularly in the 3rd and 4th cells, and an undoubted Umbra is present in the anterior cells, it seems better to designate the interspace in question as Umbro-Medial one ($U : M^1$).

The upperside of *Epinephele tithonus* (fig. 99) may be described as External, as besides the double eye-spot in the 4th and 5th forewing cells the most important part of its pattern is the terminal dark brim bordered by the third Externa (E^3) proximally. A comparison to the underside (fig. 100) leaves no doubt as to the indicated homology. A small proportion of the Umbra is present near the costa of the forewing, and a rather wide but not intense basifugal melanisation should be noted on the hindwing (*Bm*). All the other components pronounced below (E^1, E^2, M^1 in fig. 100) do not exist on the upperside. The latter undoubtedly manifests the same tendency which leads to *eversmanni* pattern in *Pararge* (fig. 52) and to that of v. *dissoluta* in *Satyrus*.

The forewing of a male *Epinephele davendra* (fig. 101) is of External type like that of *tithonus* (fig. 99) except for the fact of presence of a large androconial area (*a*) on the forewing. This area need not be classified under prototypical components being a *sui generis* element. On the hindwing of

davendra E^1, E^3, U and M^1 are readily seen though the total of the wing is considerably melanised. The underside (fig. 102) comes in support of homologies given, and it is evident again that several components present below have vanished from the upperside (M^1 on the forewing, M^2 and the eye-spots on the hindwing).

Finally the upperside of *Epinephele wagneri* (fig. 103) is nearly totally melanised but the comparatively light shade of the melanised areas should be noted in consequence of which the elongated black 5th eye-spot on the forewing is very salient. On comparing the upperside of *wagneri* to its underside (fig. 104) it becomes evident that the single eye-spot and the narrow interspace between E^1 and E^3 in the former are the only remnants of the numerous components existing in the latter. The External zone of the hindwing of *wagneri* resembles that of *davendra*. The shadow-like component accompanying the termen of the forewing most likely derives from E^3 of the underside. The possibility of participation of E^2 in the component designated E^1 in *davendra* and *wagneri* has been noted already (p. 174).

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CHAPTER VII.

REALISATION AND MODIFICATIONS OF THE NYMPHALOID PROTOTYPE IN THE GENUS APHANTOPUS.

The very small genus *Aphantopus* WALLGR. is composed after SEITZ by 3 species and 10 forms, and is very uniform concerning color-pattern. In spite of this a rather great number of prototypical components are recorded in it.

Aphantopus arvensis (fig. 106) shows three pronounced Externae (E^1, E^2, E^3), numerous eye-spots lying in the Umbra (U) which even forms Circuli (C) on the hindwing, and a first Media (M^1) bounding the wide melanised area on both wings. No components proximal to M^1 are present in *arvensis* but on the hindwing of *hyperanthus* (fig. 111) the second Media (M^2) is seen. The ocellar series of *arvensis* is completed by two *hyperanthus* specimens. In one of them (fig. 108) the 6th eye-spot is present on the forewing, in another (fig. 109) a vestigial 4th one is seen on the hindwing both being absent in fig. 106. Finally E^2 which is diffused in fig. 106 particularly on the hindwing is represented by typical narrow stripes in figs. 110, 111.

On the basis of the above data the following generic formula of *Aphantopus* may be given:

$$\frac{E^1.\ E^2.\ E^3.\ OC\ (-\ 2.\ 3.-\ 5.\ 6.--)\ U.\ M^1.\ -\ -\!-\!-\!-\!-\!-\!-\ |\ --}{E^1.\ E^2.\ E^3.\ OC\ (\ 1.\ 2.\ 3.\ 4.\ 5.\ 6.-)\quad U.\ M^1.\ M^2.\ -\!-\!-\!-\!-\!-\!-\ |\ --}$$

It consists of 21 members thus 20 out of 41 prototypical indexes being absent in it. Because the genus is very small this degree of realisation of the prototype within its limits should be regarded as very high, and the derivation of *Aphantopus* pattern from the Nymphaloid prototype is questionless. The hypothetical *Protaphantopus* is represented in fig. 105.

Let us consider now a few modifications observed in the pattern of the genus. The second Externa (E^2) is broad and diffused on the hindwing in fig. 106 being very similar to its homologue in *Epinephele pasiphaë* (fig. 94). On the forewing of the same specimen the modification is less pronounced. The cell-portions of the third Externa (E^3) are typically concave in the 4th, 5th and 6th cells in fig. 111.

Two modifications deserve attention in the ocellar series. One of them is erebisation i.e. the basipetal dislocation of the 5th eye-spot on the forewing (fig. 108). As no 4th eye-spot has been discovered in *Aphantopus* the general aspect of its "erebised" ocellar series is not very typical but the proximal position of the 5th eye-spot compared to the 6th one is conclusive enough.

On the hindwing of *Aphantopus* erebisation takes place as well. In fig. 106 the 5th eye-spot is situated nearer to M^1 and further from E^3 than any other of the eye-spots present. The rudimentary 4th eye-spot seen in fig. 109 if placed in the empty cell in fig. 106 would be exactly located between the 3rd and 5th eye-spots and thus an exact reproduction of the condition would be obtained that is seen, e.g., in the forewing of *Pararge* when the 4th eye-spot is pulled as it were by the discolating 5th one (cf. fig. 14).

Another modification is less common. Two fine pupillated eye-spots lie side by side in the 2nd cell in fig. 108. The whole of the evidence obtained from studying Nymphaloid patterns makes impossible to admit the existence of a second ocellar series, supposing the latter to be totally vanished from the huge majority of the patterns of this group of families. Hence the only alternative remains that of division of the 2nd eye-spot in transverse direction. In the subsequent chapter on *Erebia* some further evidence will be given favouring the division of ocellar components.

In the first Media of *Aphantopus* two modifications should be dealt with. One of them is the peculiar shape of the stripe on the hindwing in fig. 106. M^1 is generally rectilinear in the four posterior cells and largely concave in the anterior ones beginning with the 4th one. The principal interest of this shape of M^1 is that it resembles that occurring in some species of the Eastern Satyrid genus *Lethe*. (Schwanwitsch and Sokolov, 1934, figs. 4, 22.)

Another modification shown in fig. 111 is the basipetal dislocation of the whole of M^1 on the hindwing. The dislocating stripe meets the protruding summit of the discal cell and is divided by the latter into two independent parts, anterior and posterior. Quite similar dislocation and division resulted in have been described by me in a remote branch of the Nymphaloid group

namely in the South American genus *Opsiphanes* belonging to Brassolidae (1924, p. 521, fig. 17).

Finally a total suppresion of all the components but eye-spots and their surrounding intra-Umbral rings is observed in *Aphantopus hyperanthus* v. *bieti* (fig. 107). This is evidently due to melanisation, and a comparatively light shade of the melanised areas already noted in *Epinephele* (fig. 103) should be mentioned here as well.

The upperside of *Aphantopus* does not represent considerable morphological interest. It is strongly melanised, and the eye-spots, often depupillated, are the only components outstanding on the dark background.

CHAPTER VIII.

REALISATION OF THE NYMPHALOID PROTOTYPE IN THE GENUS EREBIA.

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The genus *Erebia* DALM. is one of the largest in the family of Satyridae. In SEITZ's Fauna palaearctica we find 179 forms of *Erebia* belonging to 66 species. There are Satyrid genera as e.g. *Mycalaesis, Euptychia* and some others which surpass *Erebia* in the number of species but they are very few. In spite of rich speciation the genus is commonly known as monotonous in color-pattern. This is dependent partly on the fact that dark hues are predominating in *Erebia* coloration, and even some homologically different patterns look rather similar. In their essence however *Erebia* patterns are very interesting morphologically, and a number of peculiar phenomena are recorded in them.

Let us see now how the prototype is realised in the genus. The patterns of *Erebia fasciata* v. *semo* (fig. 113) and *Erebia afra* (fig. 114) are very interesting from this point of view. The former shows two Externae (E^1, E^3) and very prototypical Mediae (M^1, M^2) on both wings, but it is deprived of any trace of ocellar components. Just the opposite is the case of *afra* in which a very complete series of eye-spots is present, which lacks only the 8th forewing one, but all the Externae, Mediae and Discalia have totally vanished from its pattern. A summarized formula for both above specimens is rather polynome:

$$\frac{E^1.-E^3.\,OC\,(1.2.3.4.5.6.7.-)-M^1.M^2.-----|--}{E^1.-E^3.\,OC\,(1.2.3.4.5.6.7.)\quad -M^1.M^2.-----|--}$$

There are 22 indexes in it and 19 dashes, thus *semo* and *afra* complementing each other with regard to presence of different categories of the prototypical components and showing both together a considerable degree of realisation of the prototype in the genus.

A very prototypical status shows also *Erebia lappona* (fig. 115), which has less eye-spots than *afra,* but possesses first Discalia on both wings. Its formula

$$\frac{E^1.-E^3.\,OC\,(-2.3.4.5.---)-M^1.M^2.--D^1--|--}{E^1.-E^3.\,OC\,(-2.3.4.5.--)\quad -M^1.M^2.--D^1--|--}$$

consists of 18 members being poorer than the preceding one in the eye-spots but more complete in its right half.

The only components which I am able to add to the above two formulae are the Umbra, Venosae and Intervenosae. The Umbra (*U*) on the forewing is seen in *Erebia parmenio* (fig. 169) while another *parmenio* (fig. 144) shows a very typical form of the same component on the hindwing. The Venosae and Intervenosae are sufficiently pronounced in *Erebia theano* (*V* in fig. 189, *J* in fig. 178). As to the form of components already examined in the above the following corrections should be made. In *Erebia parmenio* (figs. 116, 119) E^1 is better pronounced, and E^3 cell-portions are much less concave than in the preceding specimens. *Erebia lappona* and *manto* (figs. 117, 120) exhibit the maximum development of the first Discalis (D^1) which I have discovered in the genus; the eye-spots of *Erebia transiens* (fig. 118) are less dislocated than those on the forewing of *afra* (fig. 114) and in another *afra* (fig. 121) they are more equally sized than in the preceding one.

Now if summing up the two above formulae together with the indexes of components found in *parmenio* and *theano* (figs. 144, 169, 178, 189) the following generic formula of *Erebia* pattern is obtained:

$$\frac{E^1.-E^3.\,OC\,(1.2.3.4.5.6.--)\,U.M^1.M^2.--D^1.--|V.J.}{E^1.-E^3.\,OC\,(1.2.3.4.5.6.7.)\quad U.M^1.M^2.--D^1.--|V.J.}$$

It consists of 29 indexes, only 12 out of 41 of the prototype are absent in it, thus the realisation of the latter in the genus being sufficiently complete. The hypothetical *Proterebia* pattern (fig. 112) constructed on the basis of the generic formula illustrates the connection of the genus with prototype.

Two facts should be discussed now. One of them is the absence of the second Externa in *Erebia* generic formula. In spite of having very rich materials at my disposal I failed to discover it within the limits of the genus. This is not surprising however, since in several other palaearctic Satyrid genera the second Externa has been shown by me to be greatly inclined to disappear while the first and still more the third Externae are much more stable. One might suppose that the stripe designated E^3 in the foregoing corresponds perhaps to the second Externa of the prototype, thus supposing real E^3 to be absent. This hypothesis is, however, disproved by the great

stability of the stripe in question, by the general character of its modifications to be considered below which correspond quite with those observed in the third Externae of other genera and by its position near the Umbra. Hence I think that *Erebia* has totally lost its second Externa like the genus *Oeneis* in which I did not find it as well (1929 a, p. 626). Because, however, the latter genus is smaller and less variable in its pattern than *Erebia* the absence of the second Externa in both of them suggests the idea that perhaps in *Erebia* the tendency to the eradication of the stripe is stronger than in *Oeneis*. I mean by this that in the numerous and variable *Erebia* patterns E^2 has, so to say, more chance to manifest itself than in monotonous *Oeneis* ones. If it does not happen in either case the most plausible explanation is that the tendency to disappear is stronger in the former than in the latter.

Another fact is the presence of light veinous stripes in several *Erebia* patterns (figs. 121, 147, 149). They correspond with the Venosae of the prototype in everything but their white coloration. I have observed different prototypical components getting ochreous or red (1929 a, p. 593, 1930 a, p. 246), but in the present case there are no data at my disposal suggesting similar transformation, and until the latter is proved it should be unreasonable to homologize the white veinous stripes of *parmenio* (fig. 147) to undoubted Venosae of e.g. *theano* (fig. 189).

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CHAPTER IX.

MODIFICATIONS OF THE WING-PATTERN ON THE UNDERSIDE OF EREBIA.

The modifications which the prototype undergoes on the underside of *Erebia* are fairly various. Some of them reproduce partly or, entirely those occurring in the other genera, some others are of particular sort.

§ 1. THIRD EXTERNA.

Because the disappearance of the second Externa has been discussed already, while the first one does not exhibit anything remarkable we pass on to the third Externa.

A. Forms of cell-portions.

Like other Satyrid genera the forms of the cell-portions of the third Externa (E^3) in *Erebia* are rather different. They may be concave simple (fig. 122), convex (hindwing in fig. 180), concave bi-arcuate (posterior cells in the hindwing in fig. 195), and nearly sagittate (3rd cell in fig. 148).

B. Basipetal dislocation.

In *Erebia ocnus* (fig. 122) the position of the third Externa (E^3) and its distance from the first Media (M^1) are quite normal. In another specimen of the same species (fig. 123) E^3 has markedly shifted basipetally, and in a still another (fig. 124) the dislocation advanced very much particularly in the middle cells so that in the most cells the distance between E^3 and M^1 has become narrower than that between E^3 and the termen, the latter being very broad. Thus the dislocation is very considerable. In *Satyrus regeli* I have recorded the same process in E^3 (1929 a, p. 576) not reaching, however, such a development. On the other hand in South American Nymphalid *Perisama* (1930 a, p. 122) I have observed a basipetal shifting of E^3 which though being of different character than in *Erebia ocnus* resembles and even surpasses the latter as to the scale of the process. I mean by this that in both cases the distance is great between the initial and final positions of the dislocating component.

C. Budding.

In the 4th hindwing cell of *Erebia embla* (fig. 125) the posterior part of E^3 has formed a strong protrusion along the 4th vein. In another *embla* (fig. 126) the indicated protrusion (E^3s) has broken off from its maternal stripe (E^3) and represents now a separate component. The same tendency is readily seen also in *Erebia ocnus* v. *mongolica* and in *E. sibo*. In the latter (fig. 151) the beginning of the process takes place, as the protrusion in question is compact and not yet constricted at the base; in the former particularly fig. 149 is interesting where the E^3 protrusion in the 4th cell is hollow and constricted at the base thus exhibiting a clear form of budding of a loop from the stripe. Another case of the third Externa budding has been recorded by me in *Prepona* (1930 b, p. 323). The difference, however, is that in *Prepona* the buds are distal to E^3 and remain stationary while the stripe itself dislocates basipetally and thus separates from the buds. In *Erebia* we have seen that the case is just as opposite: the bud is proximal to maternal stripe and displaced basipetally while the latter may be regarded as stationary. Another difference is that in *Prepona* the process is of a much greater extent taking place in all the cells of the forewing.

D. Fusion with the first Media.

In *Erebia cyclopius* (fig. 127) most of the E^3 cell-portions are bent in. In the 2nd cell of another *cyclopius* (fig. 128) a broad bridge connects E^3 with the first Media (M^1) and thus the interspace between the two components is divided into two parts.

E. Partial elimination due to the incongruity of the wing and wing-pattern.

In my previous publications several facts are recorded which may be described as incongruity of the wing and wing-pattern (1930 a, p. 262). The essence of the phenomenon is that some pattern components adjacent wing-margin exhibit a shape suggesting the idea about their being cut by that margin into two parts, one really existing on the wing, and another which may be only restored in imagination for if being present it should be placed beyond the existing area of the wing. One of the best examples has

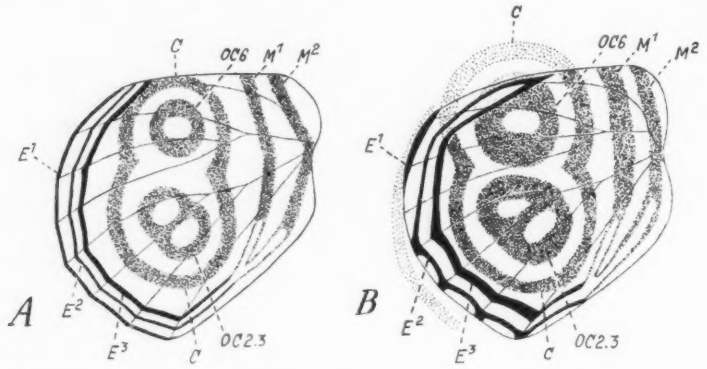

Fig. 4. Diagram of the wing-pattern of *Catagramma cunomia*. Externae (E^1, E^2, E^3) are made black, the remaining components gray. *A* Unmodified pattern. *B* Modified pattern in which E^1, *C* and *OC*6 have partly disappeared, the disappeared parts being restored in light gray; the disappearance is due partly to the location beyond the wing, partly to the destructive activity of E^3, which stripe being dislocated basipetally in the anterior cells destroys every part met of *C* and *OC*6. *C* Circulus, *OC*2. 3, *OC*6 eye-spots in the 2nd, 3rd, 6th cells resp. Other letters see text-fig. 2, p. 147. (SCHWANWITSCH, 1930.)

been found in *Catagramma cunomia* patterns, a diagrammatic representation of which is given text-fig. 4. In the diagram *A* the large eight-like pattern component *C* is placed totally on the wing. In the diagram *B* the said component has become too large to find room on the wing and therefore its anterior part is lost which according to the shape of the component should be located if present in the area anterior to the wing and which is restored in sparse dots. There are some particulars in the relation of the black stripe E^3 to *C* which are not to be explained here, as they are dealt with in another paper (1930, p. 196) and do not influence the above main result.

Erebia fasciata v. *semo* (fig. 113) undoubtedly represents an example of the same phenomenon. Let us exame first *Erebia parmenio* (fig. 144). Its third Externa (E^3), if leaving out of consideration the concavities of its cell-portions, is in general concentric with the termen being thus strongly curved down. What is especially important: the stripe does exist in the 6th

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and 7th cells, where the interspaces between it and the termen are even a little broader than in the more posterior cells. Different is the case of *semo*. On its hindwing E^3 is far from being concentric with the termen. It is much less bent than the latter and represents rather a roughly rectilinear component than a bow-shaped one. The interspaces between E^3 and the termen vary greatly in breadth being the narrowest in the 1st and 6th cells. The stripe has totally vanished from the 7th cell. In the 6th cell it is very short,

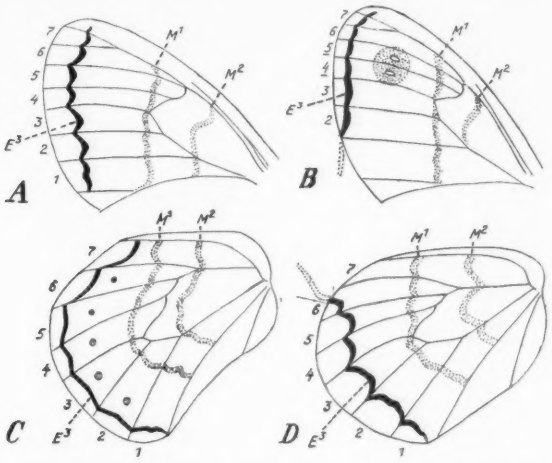

Fig. 5. Diagram of the incongruity of the third Externa (E^3) and the wing in *Erebia*. A. Normal presence of E^3 in the posterior cells of *E. fasciata* v. *semo*. B. Elimination of E^3 from the 1st cell of *E. cyclopius* owing to its supposed extra-alar location; the lost portion of E^3 is restored in dotted lines. C. Normal presence of E^3 in the anterior cells of *E. parmenio*. D. Elimination of E^3 from the 7th and the anterior half of the 6th cells of *E. fasciata* v. *semo* owing to its supposed extra-alar location; the lost portions of E^3 are restored in dotted lines. M^1 first Media, M^2 second Media, ciphers designate numbers of border cells.

begins from the 6th vein and ends abruptly at the termen being cut off by the latter as it were. It seems rather evident that the general direction of the anterior part of E^3 in *semo* crosses over the termen, and that the portion of the stripe which normally belongs to the 7th cell should be located beyond the wing on the geometrical prolongation of the existing 5th and 6th portions. The factor producing the stripe E^3 has evidently missed the 7th cell and the anterior part of the 6th one. In other words the wing and wing-pattern are partly incongruent. In principle there is no difference at all between the case of E^3 of *Erebia semo* and that of *C* in *Catagramma eunomia*.

Still another circumstance should be noted. In my paper on *Melanargia* (the idea is put forward that the transverse pattern components essentially represent a rectilinear system which becomes curved only owing to its being squeezed into radial system of veins (1931, p. 397). Besides this the property of elasticity of pattern components has been repeatedly dealt with in my

previous publications (1925, 1929a, p. 645). Being elastic they may exhibit different degrees of flexibility. In *Melanargia* e.g. the ocellar series has been shown to be stiffer than the third Externa. In *Erebia* the same stripe evidently shows two conditions. In *parmenio* (fig. 144) it is very flexible and therefore strongly bent in full correspondence with the shape of the wing-margin. In *semo* (fig. 113) E^3 is obviously much less flexible and gives the impression of a very stiff stripe. Accordingly it is not sufficiently bent to be located totally on the wing and the loss of its anterior part is the result.

As to the forewing the incongruity of the third Externa and the wing is observed in *Erebia cyclopius* (fig. 170). Its E^3 is nearly rectilinear. Because the termen is considerably curved the stripe is distant from it in the anterior cells and closely approaches it in the 2nd one. The 1st cell shows no trace of E^3 in fig. 170, and from the general form of this shortened stripe it is quite evident that its geometrical prolongation up to the level of the 1st cell would inevitably miss the wing in the above described way of the third Externa of *semo* hindwing. It is noteworthy that besides E^3 also M^1 in *cyclopius* is rectilinear, both stripes being exactly parallel. Thus evidently the rectilinear condition of stripes may be said typical of the *cyclopius* forewing. The stripes are not subdued by the influence of curvilinear system of the wing parts, and a partial incongruity of the pattern and the wing is the result.

A diagrammatical representation of the above consideration is given in the text-fig. 5. In *A* and *C* the normal course of E^3 (made black) nowhere missing the wings is figured. In *B* and *D* the hind and fore ends of E^3 resp. are located beyond the wing area and the portions of the stripe thus lost are restored in dotted lines.

On the other hand KOEHLER (1932) in his very interesting investigation on the development of wings in the mediterranean flour moth (*Ephestia kühniella*) has shown that its prepupal wing is folded in transverse direction during a few last hours before pupation, and that the bottoms of these folds represent the loci of the future stripes of expanded wings. Suppose now the same to be the case of *Rhopalocera* and of *Erebia* too, i.e., that, e.g., Externae appear in the area where the prepupal wing is folded in. If so the difference between the two Externae one wholly located on the wing and another partly missing it may be due to the different directions of the respective folds of the prepupal wings. The view put forward by KÜHN and ENGELHARDT (1933) as to the origin of the stripes of *Ephestia* pattern from some invisible determinating flux moving orderly in the pupal wing is very interesting in itself but seems to be hardly adaptable to the above cases at least at present.

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§ 2. EYE-SPOTS.

Several modifications in eye-spots should be considered nov.

A. Budding.

In *Erebia embla* (fig. 129) the 4th and 5th eye-spots have emitted each a distally directed outgrowth, which in another *embla* (fig. 130) have become fairly long but rather narrow longitudinal stripes. One could suppose that the Intervenosae of the prototype take part in the outgrowths, but this does not seem likely, as their intensely black coloration differs from that of any other pattern component of *embla* pattern (cf. fig. 195) but eye-spots.

In *Erebia afra* (fig. 131) a small black marking lies close distally to the eye-spot in the 5th cell. It seems doubtless that it has originated from the eye-spot by means of the process beginning in *embla*. Suppose the outgrowths of *embla* eye-spots to be separated from the latter the status of *afra* is the result.

In one of the subsequent paragraphs the pattern of *Erebia turanica* will be dealt with. One of its distinctive features is that the eye-spots disappear while the yellow intra-Umbral rings surrounding them remain. One of such rings, or to say better a circle (*iU*), is seen in the 3rd cell of *turanica* specimen represented in fig. 132. It shows yet a tiny vestige of its eye-spot in the centre and is of a very regular round form. In its 4th and 5th cells a large yellow marking of a complicated shape is present. It is evident that the marking derives from the common yellow area surrounding the 4th and 5th eye-spots (cf. fig. 181 in which the eye-spots are still present), and that it is emitting basifugally small circular yellow markings. In the 4th cell one marking has completely broken off, another is in statu nascendi. In the 5th cell two equally sized round markings have individualised being however yet in connection with each other and with the maternal large marking. Finally in the 6th cell a dumb-bell shaped small marking is seen evidently evolving from the division of a circular one. The undivided condition of the marking in question is readily seen in the 6th cell in fig. 183. Thus the yellow markings of *Erebia turanica* may undergo both division (in the 6th cell) and budding. Because it has been shown in the foregoing that the markings in question being of intra-Umbral origin are most intimately dependent upon the eye-spots in their size, position and form, it is reasonable to classify the above described modifications in *turanica* yellow markings under the same category of facts as the above described buddings of the eye-spots themselves described in the beginning of this paragraph.

It should be remembered that a fine case of eye-spot division takes place in *Aphantopus* (p. 183, fig. 108). Finally SÜFFERT in his recent publication (1929) has described a kind of desintegration of eye-spots in the Satyrid genus *Lethe* into a number of minute particles. On account of recently published observations upon this genus (SCHWANWITSCH and SOKOLOV, 1934, p. 159) the SÜFFERT's interpretation of this very interesting process may be fully confirmed.

The above evidence shows that there are several ways of dissolving of ocellar components into parts, and thus the existence of the processes of this sort becomes unquestionable.

B. Ereboid dislocation.

In this section we come to the consideration of a modification which has been dealt with in one of the preceding parts of the investigation (1929 a) on palaearctic Satyridae and also in the present one. The modification in question has been recorded already in six genera (*Satyrus, Oeneis, Pararge, Epinephele, Aphantopus*). Now we have to trace it in the genus which it derives its very name from.

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We have seen that by the ereboid dislocation of eye-spots or by the erebisation of the ocellar series the frequent cases are meant when on the forewing the 4th and 5th eye-spots, or only the 5th one, dislocate basipetally while all the other eye-spots remain quiescent. In *Erebia* the tendency to erebisation is so strong that it is not easy to find a specimen in which it would be totally absent. The specimens like e.g. *lappona* (fig. 115) or *ligea* (fig. 192) with their apparently undisturbed forewing ocellar series are not conclusive as they lack the 6th eye-spot which being constantly quiescent serves so to say a mark in the cases of beginning erebisation. Its absence e.g. in fig. 115 does not allow to say positively whether the 5th eye-spot is a little dislocated basipetally or not. The former alternative seems more likely. The best thing I have been able to discover in *Erebia* is *transiens* (fig. 118). Its ocellar series is but slightly modified, and the imaginary line passing through the centres of eye-spots is bent only between the 3rd and 4th ones, while the three anterior eye-spots including the 6th one are placed all on an almost straight line.

A gradual development of erebisation is easy to trace in the series of *Erebia embla* specimens (figs. 133—138). In the first of them (fig. 133) the 4th and 5th eye-spots are but very slightly displaced basipetally compared with the posterior ones. In figs. 134, 135 the said dislocation is more and more conspicuous resp. In fig. 136 the two dislocating eye-spots have considerably shifted basipetally from the general line of the remaining eye-spots. The range of dislocation is particularly evident owing to the presence of the

rudimentary 6th eye-spot not existing in the three preceding specimens. In the next *embla* (fig. 137) the dislocation has become particularly clear owing to the decrease in the yellow rings surrounding all the eye-spots. The rings of the 4th and 5th eye-spots have almost broken off from that of the 3rd one while in the preceding specimen they are widely confluent. Finally fig. 138 illustrates the climax of erebisation as observed in *embla*. The 4th and 5th eye-spots are placed far proximally from the geometrical prolongation of the line passing through the 2nd and 3rd ones.

Somewhat different form of the process is observed in *Erebia afra*. The species differs from *embla* in the great stability of the 6th forewing eye-spot which is existing in every of the four specimens represented in figs. 139—142. In the first of them (fig. 139) the minimum of erebisation discovered in *afra* is shown. In spite of the dislocation of the 4th and 5th eye-spots its ocellar series may be described yet as continuous though markedly bent in. In the next specimen (fig. 140) the 5th eye-spot has dislocated still more, the distance between it and the 6th one has become so long that the series can be hardly called continuous. In the next specimen (fig. 141) the 4th eye-spot has reached the level of the 5th one and fused with it. Finally in fig. 142 the maximum development of erebisation in *afra* is seen: the distances of the 4th and 5th eye-spots from the 3rd and 6th ones are very great. The dislocated eye-spots are situated near the middle of the interspace between the undislocated ones and the discal veins. Quite a different status exhibits our initial *afra* (fig. 139) in which the 4th and 5th eye-spots are much nearer to the remaining ones than to the discal veins.

Let us compare now the ultimate stages of erebisation reached in the two above species. In *afra* the dislocation is stronger than in *embla* which is evidenced by the fact that the distance between the dislocated eye-spots and the undislocated ones is greater in the former than in the latter. But *embla* has so to say another advantage. The most interesting result of erebisation is that it gives a misleading impression of existence of two parallel series of eye-spots. E.g. in the final *embla* pattern (fig. 138) its two anterior eye-spots might be interpreted as a remnant of one series, while the two posterior as belonging to another more distally placed. Now in *afra* (fig. 142) the 4th and 5th eye-spots form a considerable angle to the general direction of the remaining ones, while in *embla* both above indicated groups are almost exactly parallel. Hence the imitation of the would-be existence of two parallel ocellar series is better in *embla* than in *afra*.

C. Combinations.

Multi-ocellate patterns are not unfrequent in *Erebia* (figs. 114, 115, 192, 201). Bi-ocellate and uni-ocellate ones of the formulae $\frac{---4\cdot 5\cdot---}{-------}$

(fig. 197) and $\frac{- - - - - 5 - - - -}{- - - - - - - - - -}$ (fig. 202) are also not rare. On the other hand the total absence of eye-spots is very typical of a number of *Erebia* patterns (figs. 113, 174, 180, 186, 204). Thus the tendency of the elimination of eye-spots and that of retaining considerable and even high proportion of them are both strong in *Erebia*. As to the combinations which remain when the elimination is of a large scale, they partly reproduce those of the other palaearctic genera. E.g. the above formula $\frac{- - - - - 5 - - - -}{- - - - - - - - - -}$ has been recorded in *Satyrus* (1929 a, p. 584) and in *Epinephele* (fig. 98). The 4th eye-spots of the forewing so constant in *Erebia* exhibits the same property in some *Pararge* (figs. 43, 44), *Epinephele* (figs. 93, 99) and *Melanargia* (1931, figs. 2, 23, 24) patterns. The stability of the 2nd eye-spots on both wings has been established in many *Satyrus* (1929 a, figs. 141—145) as e.g. *fidia, abdelkader, dryas* and others, and recorded also in *Epinephele lycaon* (fig. 96). An indication on it may be seen also in *Erebia pronoë* (fig. 155) but the tendency is obviously less pronounced than in the two other genera.

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§ 3. MEDIAE.

A few modifications in the Mediae should be dealt with in the present paragraph.

A. Division of the Medial band.

The first of them is the transverse division of Mediae on the hindwing of *Erebia gorge* (fig. 143). The area confined between M^1 and M^2 i.e. the Medial band is markedly darker than the surrounding background; the wide interruption of it and consequently of both Mediae is readily seen in the 1st cell. In *Erebia sibo* (fig. 151) the Medial band is strongly constricted in the 1st cell. Though no actual division takes place here it is evident that in *sibo* the process is beginning which is completed in *gorge*.

The transverse division of the Medial band is not unfrequent in palaearctic Satyridae, but its most typical form is when the dividing line passes through the discal cell. According to my previous data this is the case of *Satyrus, Oeneis* (1929 a, pp. 591, 631) and *Melanargia* (1931, p. 343). But in the latter genus also the 1st cell of the hindwing occurs which resembles in a way the above described one in *Erebia* (1931, p. 349).

B. Two ways of the Medial band broadening.

In *Erebia parmenio* (fig. 144) the Medial band of the hindwing (M^1, M^2) shows rather a normal breadth and even is a little narrower than in a quite

prototypical pattern. In another *parmenio* (fig. 145) it is markedly broader, still more so it is in the next *parmenio* specimen (fig. 146), and finally in the last one (fig. 147) the distance between M^1 and M^2 particularly in the anterior cells is at least twice as broad as in the initial specimen. Thus within the limits of *parmenio* species the distance between M^1 and M^2 varies very greatly.

Another way of broadening of the same component may be seen in the next four figures. In *Erebia ocnus* v. *mongolica* (fig. 148) the condition is more or less normal. In another *mongolica* (fig. 149) the cell-portions of M^1 have become exceedingly convex. Their shapes are still more exaggerated in *Erebia sibo* (fig. 150) but besides this the general course of M^1 and M^2 has so changed that the Medial band is broad in the middle and narrowed towards the ends. In another *sibo* (fig. 151) the modification reaches its utmost degree and the general appearance of the Medial band is very peculiar.

On comparing the process in *sibo* with that in *parmenio* it should be pointed out that in the latter the removal of Mediae from each other is approximately equal in all the cells being only a little stronger in anterior ones. On the contrary in *sibo* the distance between the Mediae increases only in the middle cells, while in the anterior and posterior ones rather the opposite is the case. It seems very likely that the indicated difference depends upon that in the wing shape of the two species. In *parmenio* the form of the hindwing is normal, and does not undergo any important alteration in our series of four specimens. In *mongolica-sibo* series the wing gradually narrows. It is nearly normal in fig. 148, somewhat narrower in fig. 149, still more so in fig. 150 and markedly narrow in fig. 151. Particularly conspicuous is the narrowing in the costal area: the 6th cell is very narrow especially in its basic part, while in the 7th one the distal end is narrowed. It has been pointed out already that the pattern components may be regarded as rectilinear in their essence, and become curved owing to their being laid upon the radial system of venation. The evolution in *parmenio* and *sibo* patterns is in accordance with the indicated point of view. In *sibo* owing to the modified venation the Medial band undergoes a very strong somewhat forced bending, that is why its outlines give impression of a great strain, both in their general course and the shape of individual cell-portions. On the contrary in *parmenio* with its not altering venation the Medial band retains its more or less quiet form even in the case of maximum broadening.

An opposite tendency in Mediae i.e. that of their approximation to each other and the respective narrowing of the Medial band will be described in the next paragraph.

C. Oblique dislocation of the first Media on the forewing.

In many *Erebia* the first Media of the forewing is nearly parallel to the termen and to the third Externa (cf. M^1 and E^3 in figs. 113, 115). In *Erebia neorides* (fig. 152) the hind end of the stripe (M^1) has dislocated a little in the basifugal direction. In another *neorides* (fig. 153) the development of the indicated dislocation has resulted in an oblique position of the stripe; its hind end has almost met that of E^3, the two components forming a considerable angle. This is just the moderate degree of the oblique dislocation already recorded in the first Mediae of *Satyrus, Melanargia* and *Epinephele* (fig. 86).

D. Coalescence of the first Media and Umbra.

In *Erebia cyclopius* (fig. 170) there are seen pronounced first Media (M^1) and Umbra (U) the latter surrounding the large double eye-spot in the 4th and 5th cells and almost forming a typical Circulus. The interspace between M^1 and U is sufficiently wide. In another *cyclopius* (fig. 154) no said interspace is existing owing to the broad coalescence of M^1 with U. This coalescence is dependent upon the increase in the Umbra, or rather in the yellow zone between U and the eye-spots themselves, which seems to be the most active part of the pattern in question while the first Media remains more or less quiescent. It is obvious from the fact of the greater size of the indicated zone in fig. 154 than in fig. 170. The fact should be emphasized that in fig. 154 the Umbral circle has fused not only with M^1 but also with E^3, the latter fusion being due also to the expansion of the yellow zone and Umbral circle.

§ 4. DIFFERENT WAYS OF DARKENING.

Strong darkening of wide areas is one of the salient pecularities of *Erebia* wings, and the phenomenon of melanisation plays a more important rôle in *Erebia* than in any other genus of palaearctic Satyridae dealt with in the present work. The ways of the process in question are, however, rather numerous and some widely differing patterns are resulted in. In the subsequent sections we have to consider several examples of darkening in *Erebia* which seem to be the most interesting.

A. Melanisation in both wings.

Erebia pronoë (fig. 155) shows two Externae on both wings (E^1, E^2), two Mediae on the hindwing (M^1, M^2), first Media on the forewing (M^1)

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and several eye-spots. All the components are well pronounced and the ground is rather light.

In *Erebia sedakovi* (fig. 156) the shape and positions of the components present deviate but slightly from those of *pronoë* but owing to considerable melanisation there are some alterations in them. First of all the melanisation of the trans-External zone should be noted i.e. of the zone confined between E^3 and the termen. Owing to it no first Externa is existing more, which is pronounced in *pronoë*, while the third one (E^3) represents but a proximal limit of the indicated zone. Quite the same modification has undergone the forewing first Media (M^1) which confines the wide cis-Medial, or Medio-basal melanised area, and cannot be called a stripe, while in *pronoë* it represents a typical one. On the other hand the melanisation of the interspace between M^1 and M^2 of the hindwing should be noted, and the darkening of the basal area on the same wing wich is evidently due to basifugal melanisation.

The final status of the series is exemplified by another *sedakovii* (fig. 157). On its forewing the principal melanised areas are the same as in the preceding specimen i.e. one trans-External and another Medio-basal. They are darker than in fig. 156 but besides this the interspace $E^3 : M^1$ exhibits considerable narrowing, the latter being evidently due to corresponding dislocations of both E^3 and M^1. It is important that in spite of the interspace $E^3 : M^1$ being narrow no Umbral elements are responsible for the indicated alteration. This follows from the fact that both E^3 and M^1 retain their characteristic configuration, the former stripe exhibiting concave cell-portions, the latter (in the anterior cells) more or less convex ones. Meanwhile were the limits of the $E^3 : M^1$ area be built of the Umbra they would be undoubtedly concentric to the present large eye-spots. Only in the anterior part of $E^3 : M^1$ showing somewhat diffuse outline the participation of the Umbra is not unlikely.

The hindwing in fig. 157 is very dark with the exception of a few white ocellar markings in the 2nd and three next cells. The components E^3, M^1 and M^2 are discernible yet owing to their being still darker than the melanised background. The interspace $E^3 : M^1$ though being very dark is also visible.

B. Two ways of melanisation in hindwings.

We have now to deal with two other ways which the melanisation may follow restricting ourselves in the present section to the hindwing only.

In *Erebia ligea* v. *ajanensis* (fig. 158) there are trans-External zone (E^3) and the area between M^1 and M^2 which are melanised somewhat stronger than in fig. 156. There are, however, two distinctions from the last named specimen. The first of them is the pronounced basifugal melanisation (*Bm*), another is the presence of a typical Umbra (*U*) divided from M^1 by a well developed white $U : M^1$ interspace.

In *ligea* s.str. (fig. 159) the interspace $U:M^1$ has undergone a marked narrowing owing to the broadening of U the latter and M^1 being in contact in several cells. The Umbra itself has considerably darkened. Besides this the area Bm has approached to M^2 so that the interspace between the two so considerable in fig. 158 has become vanishing in fig. 159.

In a still another *ligea* (fig. 160) the last named interspace is totally wanting together with M^2 owing to the fusion of Bm with the second Media. The interspace $U:M^1$ so long and wide in fig. 158 has become quite narrow and its two remnants are lying one in the 4th and another in the two anterior cells. The Umbra itself has still more darkened, the eye-spots have become vestigial so that almost the total of the area distal to M^1 is uniformly dark, and only E^3 together with a couple of small depupillated eye-spots are scarcely visible in it. Thus the principal result of the described melanisation is that the slit-like vestiges of the $U:M^1$ interspace are the only well conspicuous parts of the wing-pattern.

In three specimens of *Erebia edda* (figs. 161—163) a somewhat different form of the same process is exhibited. In fig. 161 the third Externa and two Mediae (E^3, M^1, M^2) are readily seen. The white marking $U:M^1{}_4$ undoubtedly represents a remnant of the Umbro-Medial interspace thus evidently the Umbra itself and M^1 being in contact in all the cells but the 4th one. A comparison with figs. 159, 160 where also $U:M^1$ is more stable in the 4th cell than in the neighbouring ones makes the above homologisation sufficiently conclusive.

In fig. 162 general darkening is observed which covers, however, neither $U:M^1{}_4$ nor the three white ocellar markings, lying in the 2nd, 3rd and 4th cells.

The last specimen of the series (fig. 163) is very dark, the stripes E^3, M^1, M^2 are scarcely visible in it. But $U:M^1{}_4$ does not show any inclination to darkening, and in spite of being decreased in size it stands out prominently amidst the general dark together with the small ocellar marking in the 3rd cell.

Thus in both *ligea* and *edda* series $U:M^1$ represents almost the only area on the hindwing not subject to melanisation. The difference between the two cases is that in *ligea* (fig. 160) it passes over several cells while in *edda* it is restricted to the 4th one. The latter circumstance is of significance as in *Pararge roxelana* we have seen exactly the same component ($U:M^1{}_4$ in fig. 56). Consequently the stability of $U:M^1$ in the 4th hindwing cell belongs to intergeneric tendencies in our group.

C. Four parallel series of melanisation in forewings.

To show how similarly melanisation may develop in different patterns we have to consider the process on the forewings of four species of *Erebia*.

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In *Erebia embla* (fig. 164) both Mediae (M^1, M^2) are readily seen. In another *embla* (fig. 165) no trace of them is left owing to the dark background becoming still darker.

In *Erebia edda* (fig. 166) the third Externa and first Media (E^3, M^1) are still conspicuous in spite of strong melanisation of the ground. In another *edda* (fig. 167) the latter has become so dark that nothing is seen of the indicated stripes.

In *Erebia parmenio* (fig. 168) again M^1 and M^2 are well pronounced. In another *parmenio* (fig. 169) both of them have disappeared owing to the considerable advancement of general melanisation.

Finally *Erebia cyclopius* (fig. 170) exhibits the third Externa and both Mediae (E^3, M^1, M^2). In another *cyclopius* (fig. 171) the indicated stripes are absent for the background has become very dark.

Thus in four *Erebia* species the process of melanisation and of suppression of prototypical stripes develops quite in the same way. In most of the final specimens (figs. 165, 167, 171) the eye-spots surrounded by yellow intra-Umbral rings are almost the only conspicuous pattern components, and only *parmenio* (fig 169) shows still E^3.

D. Pawlowskyi pattern.

The ways of melanisation dealt with in the three preceding sections are very common in *Erebia,* and are responsible for the patterns which seem to be the most typical of the genus. In the present and the two subsequent sections we have to consider three patterns in which the melanisation develops along the lines somewhat different from the above common type.

We begin with *Erebia pawlowskyi.* One of its distinctive features is the complete absence of eye-spots. Other components, however, may be homologised rather easily. On its forewing two dark areas are seen (fig. 172), one bordered proximally by the third Externa (E^3), another lying between the first Media (M^1) and the wing basis. The last named area is fairly dark in fig. 172 but the second Media (M^2) can be discerned in it which is better pronounced in another *pawlowskyi* (fig. 174). On the hindwing (fig. 173) the third Externa (E^3) with its melanised trans-External zone is easily seen, the first and second Mediae (M^1, M^2) confine the dark area lying between them while the basifugal melanisation (*Bm*) covers the basal part of the wing. In spite of the fact of Mediae being connected by veinous protrusions with both E^2 in the posterior cells and with *Bm* in several places the homologies given for the hindwing components seem quite evident, and may be proved by comparison with e.g. fig. 156. The same is the case of the forewing. The absence of Umbra is typical of *pawlowskyi* wings, while the interspace $E^3 : M^1$ is ochreous in the forewing and creamy on the hind one.

The evolution in *pawlowskyi* principally consists in the division of the Medio-External interspace ($E^3 : M^1$) into cell-portions owing to the development of veinous stripes. In the forewing the process is of a rather restricted scale, and fig. 174 shows its maximum development recorded, the condition reached in it not being very widely different from that seen in fig. 172 where the process is not begun yet (fig. 173 shows intermediate condition between the two indicated ones). As to the hindwing the most prototypical status is seen in the four anterior cells in fig. 173 where the $E^3 : M^1$ area may be regarded as practically uninterrupted. This is not so, however, in the posterior cells of the same specimen and in all cells in the next figure, the latter showing nearly the same degree of $E^3 : M^1$ division on the hindwing as on the fore one. In the next *pawlowskyi* specimen (fig. 175) the $E^3 : M^1$ cell-portions are considerably smaller, in fig. 176 their decrease so advances that no $E^3 : M^1$ remnant can be discovered in the 1st cell. Finally in fig. 177 only three $E^3 : M^1$ cell-portions are left the rest being totally vanished. But even the existing ones are quite vestigial in the 2nd and 3rd cells. The disappearance of the interspace between the second Media and basifugal melanisation ($M^2 : Bm$) is concomitant with the above process. It develops very gradually beginning from fig. 173 and results in the total disappearance of $M^2 : Bm$ from the wing in fig. 177, so that in the latter the three $E^3 : M^1$ patches of light are the only vestiges of the pattern at all.

On comparing the just mentioned vestiges with their homologues in fig. 173 or with the wide uninterrupted $E^3 : M^1$ as seen e.g. in fig. 156 it becomes evident that the specialisation of *pawlowskyi* pattern is very high with regard to the interspace in question. The described evolution is not unparallelled however. In the forewing of *Satyrus palaearcticus* I have recorded quite a similar fusion of E^3 with M^1 on the veins (text-fig. 6). There are some distinctions between the two cases. First in *Satyrus* no melanisation takes place so that the fusing components represent perfect stripes. Second the 5th eye-spot is present in that genus which circumstance seems to prevent the stripes from approximation in the 5th and more anterior cells so that the process is restricted to the posterior ones. Meanwhile in *Erebia* owing to the absence of any ocellar components the process develops quite similarly in all the cells. But undoubtedly the essence of the modification is the same in both *Satyrus* and *Erebia*.

Finally the fact deserves attention that in *Erebia pawlowskyi* seemingly two factors are responsible for the division of the $E^3 : M^1$ area. The first of them is the appearance of veinous projections in both E^3 and M^1 which are directed to one another and become confluent on the veins. The cell-portions of E^3 and M^1 become convex and concave resp. which is not the case yet in the unmodified forewing in fig. 172. Besides this the stripes in their whole

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seem to approximate to each other which is evidenced by the fact that the distance between them in fig. 177 is much shorter than in fig. 172. Another factor is the participation of the Venosae of the prototype in the process, which seems evident as in fig. 172 the 5th and 6th veins are accompanied by pronounced stripes while M^1 in the corresponding cells shows no cellular curvations at all and those existing in E^3 are not of a sort to consider the stripes in question as deriving from the just named component. In the ultimate stages of the modification the action of Venosae seems, however, to be quite suppressed by that of the first factor. In *Satyrus palaearcticus* no participation of the Venosae has been recorded in the division of $E^3 : M^1$ area.

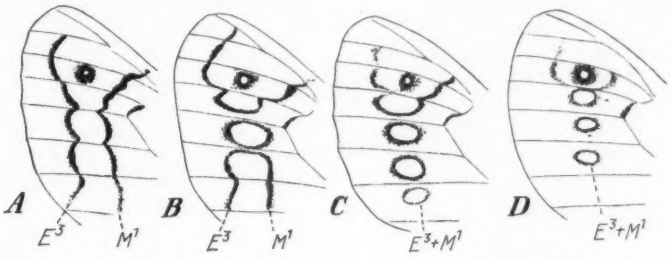

Fig. 6. Coalescense of the third Externa (E^3) with the first Media (M^1) in *Satyrus palaearcticus*. A. E^3 and M^1 are independent; B. they have fused along two veins; C. they have formed a series of rings $E^3 + M^1$; D. the latter have decreased and imitate eye-spots. (SCHWANWITSCH, 1929.)

E. Theano pattern.

The morphological composition of the pattern of *Erebia maurisius* v. *theano* (fig. 178) is the same as that of the initial forms of *pawlowskyi* series dealt with in the preceding section. Even the habitus of the indicated specimen does not deviate very widely from e.g. that of *pawlowskyi* represented in fig. 172. But the evolution in *theano* follows just an opposite direction as compared to *pawlowskyi*.

In *theano* represented in fig. 178 we see the pronounced third Externa (E^3) and two Mediae (M^1, M^2). The interspaces between the latter and that between E^3 and the wing margin are melanised. The basifugal melanisation is pronounced on the hindwing (Bm). Rather typical Venosae are present on the hindwing (V) which connect E^3 with M^2. The presence of Intervenosae (J) has been noted already when dealing with the generic formula of *Erebia*. Finally the absence of any ocellar components also belongs to the most characteristic features of *theano* pattern. All the enumerated characters except for Intervenosae have been met in *pawlowskyi*, and even some details as e.g. concave M^1 cell-portions and convex E^3 ones are the same in both species.

The next *theano* specimen (fig. 179) shows the same pattern components but they are easier to see owing to the fact of the background being considerably lighter than in fig. 178. On the other hand the narrowing of the Medial band should be noted: it is readily seen that the distance between M^1 and M^2 in fig. 179 is shorter than in the preceding one.

The above alterations are still more pronounced in the last specimen of our *theano* series (fig. 180). In both anterior and posterior wings the Mediae (M^1, M^2) are approximated to one another, so that the Medial band has become very narrow in its whole. The narrowing is especially marked on the level with the discal cells while on the forewing M^2 has so closely approached the discal veins that the two are nearly congruent. Similar modification in M^2 has been described by me in *Prepona* (1930 b, p. 344). Finally some decrease in the area of basifugal melanisation takes place in fig. 180. The result of all the modifications is that the proportion of light background areas in fig. 180 surpasses considerably that observed in the initial specimen.

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According to the above description two main processes are responsible for this result—the narrowing of the Medial band and the lightening of the background. The former undoubtedly represents a modification, as both in the prototype (text-fig. 2, p. 147) and in the *Erebia* forms which may be regarded as prototypical in their Medial band (cf. figs. 156, 158 and many others) the latter is considerably wider than in fig. 180. Different is the case of the lightening. We consider light background as prototypical status while melanisation is a modified condition, so that from this point of view the background in fig. 180 is more prototypical than that in fig. 178. Thus we come to the conclusion that in our series of specimens two processes develop in opposite directions: the narrowing of the Medial band from fig. 178 towards fig. 180 and melanisation from fig. 180 towards fig. 178. Similar interdependence is observed between the third Externa and Venosae. The latter degenerate from fig. 178 towards fig. 180, while the curvations of the E^3 cell-portions increase in the reverse sequence of figures. Thus in a series of three specimens four morphological processes develop in two opposite directions. Two of them require to place the prototype at the right end of the series, for the other two it should be placed at the left one. The case is, however, not unparallelled. In *Satyrus* I have described the gradual aquisition of convex shape in the cell-portions of the third Externa. In the same series of specimens which illustrates the process the gradual atrophy of the second Externa is demonstrated. But for the latter purpose the specimens should be traced in reverse sequence (1929 a, pp. 571, 573, figs. 18—21).

It is interesting now to compare *theano* pattern with that of *pawlowskyi*. We have seen that both morphological series begin from rather similar specimens (figs. 172, 178). Meanwhile the final conditions are widely differing, that being evident from comparison of fig. 180 with fig. 174. In

pawlowskyi (fig. 174) the broadening of the Medial band, the narrowing and division of the interspace $E^3 : M^1$ and the increase in basifugal melanisation result in a very dark pattern, while on the hindwing an almost total suppression of pattern is due to the indicated processes (fig. 177). On the contrary in *theano* the Medial band becomes narrow, the interspace between E^3 and M^1 broadens and the basifugal melanisation decreases i.e. the directions of the evolution are just as opposite to those of *pawlowskyi*. The described interrelation of the two highly specialised patterns serves a very good example showing how a given set of prototypical pattern components may evoluate in two opposite directions. A similar case of "opposite evolution" has been described by me in the South American Nymphalid *Perisama* (1930 a, p. 122).

F. Turanica pattern.

The evolution of the underside of *Erebia turanica* belongs to most exquisite processes recorded in the genus. It is not difficult to establish homologies in the *turanica* specimen represented in fig. 181. On the forewing the only pattern components are four vestigial depupillated eye-spots surrounded each by a broad yellow intra-Umbral circle (*iU*). All the other components are totally wanting owing to a strong melanisation, so that the general condition of the wing resembles those seen e.g. in figs. 165, 167. Strong erebisation deserves attention in the ocellar series the 4th and 5th members of the latter being shifted basipetally.

The pattern components of the hindwing of the same specimen are more numerous. The condition of the very complete ocellar series resembles that of the forewing, but from comparison to fig. 159 it becomes clear that the *iU* circles are situated amidst the pronounced Umbra (*U*) which shows typically diluted margin and is separated by the white $U : M^1$ interspace from the first Media (M^1). The interspace between the latter and M^2 is totally melanised, but the two stripes confining it are typical enough. The next white interspace ($M^2 : Bm$) is that between the second Media and basifugal melanisation (*Bm*), the latter being also very typical. Two facts should be noted here. One of them is the total suppresion of the third Externa due to melanisation of the corresponding areas in both anterior and posterior wings. Another is the peculiar distribution of the colors of the background, viz. the intra-Umbral circles are yellow while the interspaces adhering Mediae, i.e. $U : M^1$ and $M^2 : Bm$, are purely white.

The next *turanica* specimen (fig. 182) exhibits several differences compared with the just described one. Its eye-spots have become quite vestigial and are scarcely discernible in some of the cells. The interspace $U : M^1$ is divided into several portions by the strong stripes which have appeared on

all the veins but the 5th one. In the $M^2 : Bm$ interspace its disappearance from the 7th cell should be noticed.

In the next *turanica* (fig. 183) the last named interspace has disappeared at all, while the portions of the $U : M^1$ have much decreased in size and show very irregular and various shapes. A contraction of the *iU* circles should be mentioned as well. The general habitus of the specimen is peculiar especially that of its hindwing, where a number of white and yellow markings shaped very differently are scattered apparently without definite order. The above derivation shows, however, where they evolve from. The next *turanica* (fig. 184) is interesting as it is more advanced in some respects than the preceding one. Its $U : M^1$ markings exhibit considerable degeneration. They have disappeared from the majority of the cells being present only in the three middle ones, and the retained portions are of very irregular forms. Besides this the degeneration of eye-spots has become still more complete. In fig. 183 several tiny rudiments of them can be seen yet, while in fig. 184 only one is seen in the 1st hindwing cell, the rest being totally absent. But on the other hand there are undoubted backward features seen in fig. 14. They are the presence of $M^2 : Bm$ totally absent in fig. 183 and the general hue of the melanised areas which is considerably lighter than in any of the three preceding *turanica* specimens.

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CHAPTER X.

UPPERSIDE PATTERNS IN EREBIA.

§ 1. GRADUAL MELANISATION.

In the present chapter several upperside patterns of *Erebia* will be dealt with which appear the most typical and interesting. Let us begin with *Erebia lappona*. Its underside (fig. 191) belonging to the most prototypical in the genus exhibits the third Externa (E^3), Mediae (M^1, M^2) and first Discalia (D^1) all sufficiently pronounced on both wings. The ocellar series is rather polynome and consists of four depupillated eye-spots on each wing. The upperside of the same specimen (fig. 190) also represents the most prototypical condition which I was able to discover among the upperside patterns of *Erebia*. Its forewing shows the same eye-spots and stripes as the underside. The Mediae and Discalis are even better pronounced in fig. 190 than in fig. 191 as their posterior ends lost in the latter are existing in the former. But the coloration of the ground is different on the two surfaces. On the underside it is more or less uniform except for the darkish *Bm* area, the 1st cell and the striolated costal and terminal zones. On the upperside the areas one proximal to M^1 another distal to E^3 are markedly darker than

the interspace $E^3 : M^1$ situated between the two stripes. The melanisation in the indicated areas is not strong so that no stripe is lost bordering them or lying in them. But nevertheless the melanisation is of importance for the habitus of the forewing so that the latter may be evidently classified under Medio-External type of pattern to which e.g. the forewings of *Pararge adrastoides* (fig. 44) or *Epinephele pasiphaë* (fig. 93) are belonging.

The hindwing upperside of *lappona* deviates much greater from its underside than it is the case in the forewing. Out of many components present on the underside only three eye-spots have reached the upperside all the rest of the wing being totally melanised. The eye-spots are, however, somewhat larger than their underside counterparts and light intra-Umbral rings (*iU*) surround every of them.

It has been pointed out already that in some cases the Umbra and the melanised areas show close affinity and no exact distinction can be drawn between them. It does not mean that the two components are identical, and the problem of their complicated interrelation is not to be discussed in the present paper. But in any case the light circum-ocellar rings like those of *lappona* and of many other *Erebia* may be surrounded either by undoubted Umbra (figs. 2, 30, 104) or by typical melanised area (fig. 196). In both cases their characters remain the same, viz. the rings are exactly concentric to the eye-spots, their breadth is moderate, and ochreous yellow coloration is the most typical of them. Because the rings are very frequent in many genera it is necessary to name them provisionally even before the interrelation between the Umbra and melanised areas is sufficiently elucidated. The above used name of intra-Umbral rings or interspaces seems to be the most suitable.

Thus on the hindwing of *lappona* upperside (fig. 190) the three eye-spots with their intra-Umbral rings (*iU*) are the only existing pattern components. Because, however, on the forewing the components are more numerous and do not deviate greatly from the prototypical status, the general appearance of *lappona* upperside is rather prototypical. If even in the most prototypical form of the genus *Erebia* the melanisation is as much pronounced as to suppress nearly all the hindwing pattern components this is an indication of the great rôle which the process in question plays in the genus.

In *Erebia ligea* we already see a much more advanced melanisation on both sides of the wings. On its forewing underside (fig. 193) the area proximal to M^1 and that distal to E^3 are totally melanised without any trace of other stripes left in them, and it is obvious that the interspace between the two named stripes is Medio-External ($E^3 : M^1$). On the upperside the just described condition of the forewing is reproduced rather exactly (fig. 192). As to the hindwing its underside differs from that of the forewing (fig. 193). There are seen typical second Media (M^2) and the area of basi-

fugal melanisation (*Bm*) which are lacking on the forewing. On the other hand the hindwing shows a pronounced Umbra (*U*) which is, however, so dark that the third Externa (E^3) passing between it and the darkened trans-External zone has become almost invisible. Practically between the white Umbro-Medial interspace ($U:M^1$) and the termen there is one broad dark area in which several eye-spots are situated surrounded each by a typical yellow ring. But on the upperside (fig. 192) the eye-spots are placed in the yellow area designated $E^3:M^1$. On comparing the latter with fig. 193 it becomes obvious that its proximal boundary follows closely the line occupied by M^1 on the underside. The distal boundary of the same area corresponds rather exactly to the position of the scarcely visible remnants of E^3 on the underside. Thus we come to the conclusion that the difference between the upper and under sides in *Erebia ligea* is much greater in the hindwing than on the forewing. We have already seen that in the latter the two surfaces are nearly identical. On the contrary in the hindwing *Bm*, M^2 and *U* present below have vanished from above, E^3 well pronounced above is scarcely visible below, the light ribbon is yellow $E^3:M^1$ above and white $U:M^1$ below. The particular interrelations existing between the four wing surfaces in question may be briefly described as follows. Medio-External pattern viz. yellow $E^3:M^1$ ribbon with the eye-spots in it is existing in three surfaces namely in the forewing upperside, in the forewing underside and in the hindwing upperside. Umbro-Medial pattern viz. white $U:M^1$ with the eye-spots distal to the latter is restricted to one surface only namely that of the hindwing underside. This is of course an example of the *Argynnis* type of OUDEMANS' phenomenon which will be discussed in the chapter XVII.

Erebia embla shows another more common type of the upperside melanisation than *ligea* does. On its hindwing underside (fig. 195) characteristic Mediae (M^1, M^2) and basipetally dislocated third Externa (E^3) are readily seen. The dark striolated ground filling up the area between M^1 and E^3 evidently corresponds to the Umbra though the fact deserves attention that it does not differ at all from that between E^3 and the termen. On the basis of the foregoing analysis (cf. figs. 161, 163) the white marking $U:M^1{}_4$ is obviously a remnant of the Umbro-Medial interspace which is so large e.g. in the preceding species (fig. 193). None of the just described stripes and interspaces are present on the upperside of *embla* hindwing the total of it being completely melanised (fig. 194). On the forewing M^1 and E^3 are pronounced below (fig. 195) and the interspace between them is as dark and striolated as on the hindwing with the difference that the strioles are absent in the posterior cells. Four fine eye-spots are placed in the same interspace which are encircled by a continuous yellow area (*iU*), the latter being evidently concentric to them. They evidently represent four intra-Umbral rings fused together. These rings together with their eye-spots are the only pattern

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components present above since the Externa and Media have totally vanished from the upperside of the forewing (fig. 194). Thus the upperside of *Erebia embla* may be very briefly described: it exhibits four eye-spots with their coalesced Umbral rings on the forewing while all the rest of both wings is totally melanised.

A similar but somewhat more advanced condition is observed in *Erebia cyclopius*. Its underside (fig. 197) is still simpler than that of *embla*. On the hindwing the two Mediae (M^1, M^2) and third Externa (E^3) are the only important components while on the forewing nothing is left of them and the pattern is restricted to the pair of coalesced eye-spots surrounded by the common intra-Umbral ring (*iU*) which is strongly expanded and shaped very exactly circular. The two eye-spots and intra-Umbral ring are the only pattern components existing on the upperside of *cyclopius* (fig. 196) the rest of both wings being completely melanised. It should be only remarked that the eye-spots are a little larger in fig. 196 than in fig. 197 while just the opposite is the case in the *iU* ring.

A still further progress in the same direction is seen in *Erebia hades*. As to its underside (fig. 199) the forewing does not differ homologically from that of *cyclopius* (fig. 197) showing only a lesser breadth in the *iU* ring. On the hindwing the first Media (M^1) is the sole stripe present but the existence of a very complete series of ocellar markings should be noted which replace true eye-spots. The upperside of *hades* (fig. 198) is still more melanised than those of the two previous species. Its hindwing does not differ from those of the latter showing also no trace of any pattern component. On the forewing the disappearance of the intra-Umbral ring is important. The only readily seen thing on *hades* upperside is the large white pupil of the 5th eye-spot. Meanwhile the eye-spot itself is hardly discernible being only quite a little darker than the surrounding melanised area and not being separated from the latter by any interspace. The pupil of the 4th eye-spot well pronounced below does not reach the upperside at all. A somewhat darker shade of melanisation in *hades* should be also noticed compared with the preceding forms.

The final stage of the process under consideration is very simple. It consists of a total absence of pattern components on both sides of both wings, and may be seen in *Erebia manto* v. *constans* (figs. 203, 204). This remarkable status is evidently due to the strong melanisation, and the only difference to be noted between the upper and under sides is that the former (fig. 203) is darker than the latter (fig. 204). This is, however, in accordance with the interrelations already recorded in the previous forms of *Erebia*.

The processes dealt with in the present paragraph belong to the main direction of the evolution on the upperside of *Erebia* wings, which may be recapitulated as follows. Melanisation covers first the areas of wings lying outside of the Medio-External interspace (fig. 192). Than the latter also

undergoes melanisation except for the intra-Umbral rings (figs. 194, 196), which disappear in their turn leaving visible only an eye-spot (fig. 198), and finally everything vanishes (fig. 203). The first and second phases of the indicated evolution, i.e. the Medio-Externas and intra-Umbral patterns, seem to be particularly typical of the genus. We have to consider now a few other directions in the evolution of *Erebia* upperside.

§ 2. MULTIOCELLATE PATTERNS.

There are some uppersides in *Erebia* which show a great completeness in their ocellar series. One of them is *Erebia afra* (fig. 187). Its ocellar formula is $\frac{1.2.3.4.5.6.--}{1.2.3.4.5.--}$ i.e. eleven out of fifteen prototypical eye-spots are present and only four are absent. (On the underside there are two eye-spots more—fig. 114.) The eye-spots of *afra* are strong and represent the sole conspicuous prototypical component all the stripes except D^1 being absent. On the hindwing the eye-spots are surrounded by intra-Umbral rings. The apical area of the forewing is of a considerably lighter shade than the rest of both wings which is most likely due to melanisation not having spread all over the forewing. In the general appearance of *afra* the eye-spots with their bright pupils undoubtedly play the most important rôle and thus the pattern may be defined as multiocellate.

Another bearer of the same type is *Erebia medusa* (fig. 200). Its eye-spots are less numerous than those of *afra*. There are eight of them. As to the other components the presence of typical intra-Umbral rings (*iU*) on the hindwing is doubtless. On the forewing the same is the case in the 2nd cell, but in the more anterior ones the outlines of the yellow circum-ocellar areas are not concentric to the respective eye-spots and rather broad for which reason their most plausible homologisation is to consider them as remnants of the Medio-External interspace ($E^3 : M^1$). The indicated homology is however not quite proved owing to the remakable fact of a very complete resemblance of the two sides of *medusa*. On its underside (fig. 201) there are no more stripes than on the upper one. Other specimens of *medusa* which have been at my disposal show the stripes only on the hindwing underside thus not facilitating the analysis of the forewing. Finally the fact deserves attention that in *afra* (fig. 187) the ocellar series shows most typical form of erebisation while in *medusa* but a very slight inclination to this process may be discovered.

We have to return now to *Erebia turanica* whose underside has been described in the preceding chapter (p. 203). The upperside of *turanica* like those of *afra* and *medusa* belongs to multiocellate type but the fact should be emphasized that the eye-spots themselves have vanished from it. We have

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seen that on the underside of *turanica* (fig. 184) there are two main series of light markings, one consists of white Umbra-Medial interspaces ($U:M^1$), another of yellow intra-Umbral circles (iU) from which the respective eye-spots have disappeared. This is the case of the hindwing while on the forewing only the last named intra-Umbral series is present. The upperside of *turanica* (fig. 185) differs from the underside (fig. 184) in having totally lost any markings but the intra-Umbral ones. The latter retain typical arrangement of an ocellar series in spite of the absence of eye-spots. E.g. on the forewing in fig. 185 the intra-Umbral markings have undergone most characteristic erebisation viz. the iU circles of the 4th and 5th cells are dislocated basipetally. On comparing *turanica* with *afra* (fig. 187) it becomes obvious that the process of erebisation is the same in both of them with the only difference that the dislocating force acts upon the genuine eye-spots in the latter and on the intra-Umbral markings in the former. Thus the description of *turanica* upperside may be given in a somewhat paradoxial form namely the pattern is typically multiocellate though no ocelli (eye-spots) are present in it.

The just described pattern serves a starting point for a still another modification. Fig. 186 represents a *turanica* specimen in which the most of the forewing intra-Umbral circles have strongly expanded and fused with each other having thus formed a large yellow marking exhibiting clear traces of its origin. But the small intra-Umbral circle of the 6th cell shows no increase at all and therefore remains independent. The general appearance of the pattern resulted in is rather widely differing from that of typical *turanica* (fig. 185) but their closest morphological affinity is sufficiently clear.

§ 3. INOCELLATE OR LONGITUDINAL PATTERNS.

We have examined already the underside pattern of *Erebia theano* (fig. 180). The upperside of the same specimen is represented in fig. 189. It is remarkable how slight is the difference between the two surfaces of its wings. There are only two distinctions to be noted here. One of them is that the melanisation is somewhat more pronounced on the upperside than on the underside which is easy to see in the Medial band (M^1, M^2), in the zone between E^3 and the termen, and in the area of basifugal melanisation (Bm). On the other hand the Venosae (V) represent rather pronounced stripes in fig. 189 which is not the case in fig. 180. They play a considerable rôle in the habitus of the upperside owing principally to the breadth of the $E:M^1$ interspace, while the Medial band is narrowed in *theano* compared with other *Erebia* forms (cf. e.g. fig. 190). That is why *theano* pattern may be described as longitudinal. Because neither eye-spots or any ocellar components are present in it the term of inocellate pattern also suits to it.

Erebia pawlowskyi represents another example of the same type. We have

seen already that the fragmentation of the Medio-External interspace ($E^3 : M^1$) into cell-portions and the nearly total melanisation of the rest are its salient characters (figs. 172—177). This underside serves a basis for the upperside the difference between the two being restricted to the general decrease of the $E^3 : M^1$ fragments and to the total disappearance of all the other interspaces as it is ready to see in fig. 188. The upperside habitus of *pawlowskyi* differs much from that of *theano* (fig. 189) which is due principally to the fact that $E^3 : M^1$ interspaces are small in the former and very wide in the latter, and also to the total melanisation of the Medio-basal area in *pawlowskyi* which yet exhibits wide yellow markings between M^2 and Bm in *theano*. But the homologous resemblance of the two patterns is very close the $E^3 : M^1$ interspace being of prime importance in both of them. On the other hand the general appearance of *pawlowskyi* upperside resembles greatly that of *turanica* (fig. 185). In both of them the pattern consists of series of small ochreous markings on the dark background. The most conspicuous difference between them is that on the forewing of *turanica* the markings are shifted basipetally in the 4th and 5th cells, that being not the case in *pawlowskyi*. But we have seen already that the markings in question are totally different in the two species concerning their homology since they are intra-Umbral (iU) in *turanica* and Medio-External ($E^3 : M^1$) in *pawlowskyi*. Thus we come to an interesting conclusion that *pawlowskyi* and *turanica* uppersides (figs. 188, 185) are homologically different but look very similar, while *pawlowskyi* and *theano* (figs. 188, 189) look quite different in spite of their closest homologies. But it is noteworthy that the enlarged iU markings on the forewing of another *turanica* (fig. 186) imitate in a way the wide yellow $E^3 : M^1$ area of *theano* (fig. 189).

§ 4. DEVELOPMENT OF LIGHT AREAS.

Some peculiar phenomena take place in *Erebia mani* and related patterns.

On the underside of *Erebia mani* v. *fasciata* (fig. 210) a characteristic first Media (M^1) forms the limit of the dark Medio-basal area. In another *mani* (fig. 209) the indicated area has undergone some depigmentation in its distal zone. The process is especially pronounced in the 4th and 5th cells, where the Medio-basal area is considerably lighter than in the discal cell, and the discal veins serve a dividing line between the dark and light parts of the area. The stripe M^1 has lost therefore its typical character and has become diffused. On the upperside of the same specimen (fig. 206) the indicated pecularities are still more pronounced: the dark pigment has almost vanished from the basal ends of the 4th and 5th cells, so that the anterior part of the dark area can be hardly called Medio-basal but rather Disco-basal. In the posterior cells the border of the area is so diffused that the

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very existence of M^1 in fig. 206 becomes doubtful. A still stronger diffusion is observed on the upperside of *mani* v. *fasciata* (fig. 208) whose underside (fig. 210) is referred to already.

A further advance shows *Erebia herse* (fig. 207). The depigmentation begun in *mani* (fig. 206) has led to almost total of the discal cell becoming yellow, while the dark basal area is concentrated in the dorsal region of the wing. The limit of this area cannot be exactly compared with any components of the prototype though the participation of M^1 in its 1st cell portion cannot be absolutely denied. More important, however, is that the dark area in question derives most likely from the basifugal melanisation, which, as it is recorded in my paper on *Melanargia* (1931, p. 384) tends to develop quicker in the posterior cells of the forewing than in the anterior ones.

The last pattern to be examined in the present paragraph is that of a non identified form of *Erebia mani* (figs. 202, 205). Its forewing does not differ substantially from that of *mani* (fig. 206) except for the white coloration in the place of yellow one. But the hindwing is peculiar. Instead of being totally melanised (figs. 206, 207) it shows a broad white peripheric zone (fig. 205) whose proximal boundary is roughly rectilinear, diffused and evidently does not depend upon the typical M^1 seen on the underside of the same specimen (fig. 202). Therefore the dark part of the hindwing upperside of *Erebia mani* var. should be also regarded as deriving from basifugal melanisation (*Bm*). Finally it should be remarked that a typical External dark brim bordered by E^3 proximally is present in all the wings dealt with in the present paragraph with the exception of the hindwings in fig. 205. The dark diffused area near it in figs. 208, 210 possibly corresponds to the Umbra.

In general the upperside of *Erebia mani* and related patterns may be described as follows. The area of basifugal melanisation generally shows diffused margins (fig. 207, *Bm*). But if a strong first Media is present the melanisation fills up the total of the interspace between M^1 and the wing basis, thus the stripe, shaping very sharp the margin of the area (fig. 210). But if M^1 undergoes degeneration the said margin becomes diffuse (fig. 209) and the area itself disappears from the anterior cells (figs. 206, 207). Similarly on the hindwing the outer margin of the *Bm* area is very diffused in fig. 205 owing to the absence of prototypical stripes, the latter being represented only by the vestigial interveinous stripes particularly clear in the 3rd cell.

Thus in the present case on the one hand there is a sort of dependence between the prototypical component i.e. the first Media and the melanisation. Until the former is present it holds, as it were, the latter within the prototypical limits. When it disappears the basifugal melanisation is set free and its shape not corresponding to any components of the prototype is the result.

Thus on the other hand the idea is get about some independence of the factors of basifugal melanisation from those of prototypical components. In *Epinephele lycaon* we have seen an example of a still greater independence of the basifugal melanisation from prototypical stripes.

CHAPTER XI.

REALISATION OF THE NYMPHALOID PROTOTYPE IN THE GENUS COENONYMPHA.

The genus *Coenonympha* HBN. consists according to SEITZ's Fauna palaearctica of 23 species and 70 forms being thus one of large genera in the family of Satyrids. Let us see now which is the representation of the prototype in *Coenonympha*.

On comparing *Coenonympha saadi* (fig. 212) with the prototype it is easy to see in it the narrow and rather light first Externa (E^1) on both wings and the series of eye-spots which are numerous and pupillated on the hindwing, while on the forewing only that in the 5th cell is provided with a pupil, the two others being enlarged and depupilated. The eye-spots are surrounded by the typical Umbra (U). Proximally to the latter a pronounced first Media (M^1) passes across both wings.

Between the first Externa and the eye-spots a broad stripe passes designated E^3. It is white in the figure while in the specimen it consists of silvery scales like those composing the well known markings on the underside of many *Argynnis* forms. On the basis of the evidence to be given in the subsequent description I consider the silvery stripe of *Coenonympha* to be a homologue of the third Externa of the prototype. If putting together the indexes of all the above prototypical components the following pattern formula of *Coenonympha saadi* is obtained:

$$\frac{E^1.-E^3.\,OC\,(-2.3.-5.---)\;U.\,M^1.-------|--}{E^1.-E^3.\,OC\,(1.2.3.4.5.6.-)\quad U.\,M^1.-------|--}$$

The symbols of 17 components out of 41 which the prototype is built of are present in the formula thus the 24 absent ones being replaced by dashes.

Like other similar cases the above formula can be made more complete if taking into consideration other forms of the genus. To begin with the Externae it should be pointed out that *Coenonympha thyrsis* (fig. 224) shows a rather typical third Externa (E^3) in the place of the above indicated silvery stripe of our initial specimen. A detailed consideration of the transmutation of a common dark stripe into a silvery one will be given in the next chapter. In this place it should be remarked only that the general character of the

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stripe in question as seen in fig 224, its position on the wing and its immediate contact with the Umbra (*U*) are sufficient to make conclusive the proposed homologisation, as in a number of other cases undoubted third Externae show exactly the same features. As to the second Externa I was not able to discover any undoubted traces of it in *Coenonympha* that not being surprising owing to the general tendency of this stripe to disappear. Finally the first Externa (E^1) is represented by a very dark stripe in another specimen of *Coenonympha thyrsis* (fig. 225) being in it more typical than in fig. 212.

As to the eye-spots a very complete series of them is present in *Coenonympha amaryllis* (fig. 214). The ocellar formula of the latter is $\frac{OC\ (-2.3.4.5.6.--)}{OC\ (1.2.3.4.5.6.-)}$; all the eye-spots are well pronounced and pupillated. In *Coenonympha oedippus* (fig. 216) the 1st eye-spot of the forewing is seen, in *Coenonympha sunbecca* (fig. 215) a fine series of intra-Umbral markings (*iU*) is seen, one of the latter being present in the 7th cell. The best though somewhat paradoxical description of *sunbecca* wing is that its intra-Umbral markings are exactly concentric to the totally absent eye-spots. Thus it is evident that the ocellar factor is at work in the 7th cell of *sunbecca* though its action is apparently not sufficient to produce a genuine eye-spot. Finally the duplication of the 1st eye-spot on the hindwing of *Coenonympha hero* (fig. 217) should be noted which is very common in the 1st cells of both wings. If summing up the above data on the eye-spots the formula $\frac{OC\ (1.2.3.4.5.6.--)}{OC\ (1.2.3.4.5.6.-)}$ should be given for *Coenonympha* with the notion that in the 7th forewing cell an undoubted tendency of the appearance of eye-spot is undeniable.

We have seen only the first Media (M^1) in fig. 212. Meanwhile in *Coenonympha myops* also the second one (M^2) is present. On the hindwing it is very typical (fig. 219) and together with the first one (M^1) forms a characteristic symmetrical pair. On the forewing it (fig. 218) is less typical being markedly suffused, but nevertheless its homologisation is unquestionable. *Coenonympha myops* does not belong to the typical representatives of the genus. But the second Media has been also discovered in some other more characteristic *Coenonympha* forms. On the hindwing of *C. corinna* (fig. 221) a very fine M^2 is seen. The anterior portion of the stripe wich has disappeared owing to the melanisation of the 7th cell is readily seen in another *corinna* specimen (fig. 220).

A first Discalis (D^1) is present on the underside of the forewing of *Coenonympha myops* (fig. 219), being better pronounced on the upperside in *C. leander* (fig. 222). On the hindwing of the former (fig. 219) a slight vestige of the first Discalis (D^1) is conspicuous. As to the longitudinal stripes

only Venosae (V) may be seen in the forewing of *Coenonympha leander* (fig. 223).

If adding to the above pattern formula of *Coenonympha saadi* the indexes of the second Media and first Discalis of *Coenonympha myops* (figs. 218, 219), that of Venosae of *C. leander* (fig. 223) and those of several eye-spots seen in *C. amaryllis* and *oedippus* (figs. 214, 216) the following generic formula of *Coenonympha* is obtained:

$$\frac{E^1.-E^3.\,OC\,(1.2.3.4.5.6.--)\;U.\,M^1.\,M^2.--D^1.--|\,V.-}{E^1.-E^3.\,OC\,(1.2.3.4.5.6.-)\quad U.\,M^1.\,M^2.--D^1.--|--}$$

It contains 25 indexes, thus 16 components out of 41 of the prototype being absent in the genus *Coenonympha*. This degree of the realisation of the prototype is quite sufficient to illustrate the immediate bearing of the latter upon the genus under consideration. The hypothetical *Protococnonympha* (fig. 211) shows the connection of the two still better than the formulae.

Let us add a few words about the components absent in *Coenonympha*. The absence of the second Externa is an important fact especially in such an extensive genus. But it should be remembered that the same is the case of the still greater genus of *Erebia* while the general tendency of the stripe to degenerate has been already mentioned. Also important is the absence of the second Discalia and Basalia, as these components belong to the important parts of the prototype.

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CHAPTER XII.

MODIFICATIONS OF THE WING-PATTERN ON THE UNDERSIDE OF COENONYMPHA.

In the present chapter we will consider the most interesting modifications which the prototype undergoes on the underside of *Coenonympha*.

§ 1. ARGENTATION OF THE THIRD EXTERNA.

The third Externa exhibits a remarkable modification in *Coenonympha*. We have already seen that the third Externa (E^3) of *Coenonympha thyrsis* (fig. 224) is rather normal. It is dark, rather broad and shows concave cell-portions typical of this stripe in general. In another *thyrsis* (fig. 225) E^3 shows the same general shape. But the structure of the stripe is different. The prototypical status is retained only in the 1st cell of the forewing where E^3 is totally dark and rather narrow. In the next cell, however, the stripe has splitted longitudinally into distal and proximal halves, and a narrow

interspace lies between them filled up with the scales of metallic silvery coloration. In the 3rd cell of the same wing the silvery interspace has somewhat broadened and the distal half of the stripe is considerably narrower than the proximal one. The same condition is still more pronounced in the majority of hindwing cells where the silvery interspace is fairly broad, the proximal dark half is easy to see while the distal one has nearly vanished.

Similar process is observed in *Coenonympha amaryllis*. In one specimen of it (fig. 226) the forewing E^3 is very prototypical being quite narrow in the anterior cells and showing no traces of silvery coloration at all. In the forewing of another *amaryllis* specimen (fig. 227) E^3 consists af a narrow silvery stripe accompanied by a still narrower dark one. The latter passes along the proximal border of the silvery stripe, the distal one being devoid of any presence of dark pigment. In a still another *amaryllis* (fig. 228) both the dark part of E^3 and still more the silvery one have markedly broadened. The hindwings of the three *amaryllis* specimens reproduce the just described evolution of the fore ones beginning it, however, at a somewhat later stage, namely the hindwing E^3 of fig. 226 is in the condition of the forewing E^3 of fig. 227, i.e., consists of distal silvery and proximal dark halves. In the next two specimens a strong widening of both indicated parts of E^3 is seen, which is again particularly pronounced in the silvery part. It should be remarked that in the last *amaryllis* specimen the broad silvery stripe plays a considerable rôle in the general habitus of pattern.

Finally in *Coenonympha oedippus* the same process of "argentation" may be traced. In fig. 229 the 1st forewing cell exhibits narrow dark E^3, without any conspicuous tendency to the appearance of silvery coloration in it. But in the 2nd and more anterior cells of the same wing the stripe, retaining nearly the same breadth, consists, however, principally of silvery scales, the dark ones forming an extremely narrow and even not quite uninterrupted line along the distal border of the silvery area. The same condition is existing in all the hindwing cells. In the next *oedippus* specimen (fig. 230) the silvery stripe has broadened which is not the case, however, of the dark lines, which are as narrow as in the preceding figure; it should be only remarked that in the hindwing the dark scales are visible on both sides of the silvery area. The latter increases much in breadth in a still another *oedippus* specimen (fig. 231) forming one of the most conspicuous components of the pattern, like it is the case of *amaryllis* (fig. 228). It should be added that the dark parts of E^3, tiny in the above *oedippus* specimens, may totally disappear from the pattern which may be seen both in *oedippus* (fig. 242) and in some other species too, as e.g. in *arcania* (fig. 245).

What may be interpretation of the described facts? The simplest one is to assume that the third Externa undergoes longitudinal division, the background between the two halves thus arisen becomes silvery, the halves them-

selves disappear while the silvery area persists and becomes broad. From this point of view the latter differs in nothing but its coloration from the other interspaces present on the wings as e.g. that between U and M^1 or iU circles, and according to the system adopted in my previous publications it should be designated $E^3d : E^3p$ meaning by E^3d and E^3p the distal and proximal halves of the third Externa respectively. This interpretation is, however, not quite plausible. There are two reasons against it. One of them is that when a stripe divides itself the halves resulted in usually remove from each other. But, e.g., on the forewing in fig. 229 the silvery stripe in the 2nd cell is of the same breadth as the dark one in the 1st cell, thus evidently both divided and undivided parts of the component being equally narrow. On the other hand the division of stripe does not imply yet its atrophy. Meanwhile we have seen that in *Coenonympha oedippus* (fig. 229) the amount of dark pigment in E^3 becomes extremely small when the silvery coloration appears, and the dark coloration disappears totally (fig. 242). From the above viewpoint of the division of E^3 that means that the stripe itself vanishes, and only the interspace between its halves persists. I think that the above data may be interpreted otherwise. It seems likely that the third Externa in *Coenonympha* does not undergo longitudinal division but only changes its prototypical dark coloration into silvery one. This process of "argentation" begins either in the middle line of the stripe (figs. 225, 229) or at its distal margin (figs. 226—228). The former way resembles division, the latter does not. From this point of view the silvery stripe of *oedippus* (fig. 231) represents not an interspace between two halves of E^3 but the stripe itself, while in *amaryllis* (fig. 228) E^3 should be regarded as consisting of two parts: the distal part is "argentated", the proximal one retains its prototypical dark coloration and shows typical concavities in the cells. I do not consider this interpretation as final, possibly a still another more adequate may be offered, but as a working hypothesis it seems to fit the facts better than that of division.

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§ 2. FUSION OF THE THIRD EXTERNA AND CIRCULI.

Let us now pass on to a peculiar modification observed in the Circuli of *Coenonympha*. In *Coenonympha hero* (fig. 232) the series of Circuli is well pronounced (dC, pC). Because the eye-spots of *hero* are large the corresponding Circuli have undergone fusion so that in the majority of the cells the distal halves of Circuli (dC) have separated from the proximal ones (pC). The fact should be noted that both halves of a given Circulus, e.g. of that lying in the 3rd cell are of nearly equal size and breadth. Different is the case in the next *hero* specimen (fig. 233) in which the proximal halves of the Circuli (pC) have become heavy while the distal ones (dC) are ob-

viously degenerating and show considerable approximation to the argentated third Externa (E^3). The indicated approximation is still more pronounced in the next *hero* (fig. 234) the distal halves of the Circuli (*dC*) and the silvery E^3 are in contact in several places but the dark proximal border of E^3 is still discernible. In the next *hero* (fig. 235) *dC* cannot be discriminated from the dark border of E^3, the two being totally fused. The Circuli, however, still preserve their individuality which follows from the fact that the yellow intra-Umbral interspaces (*iU*) exhibit their typical shape concentric to the eye-spots, and consequently the Circuli shaping the periphery of the interspaces do exist in all their parts. This is hardly so in the next *hero* specimen (fig. 236). Only the proximal halves of its *iU* interspaces are concentric to the eye-spots being bordered by the falciform proximal halves of the Circuli (*pC*). Meanwhile the distal parts of *iU* are bordered by E^3, the latter not being concentric to the eye-spots at all. If even some elements of the Circuli still exist in the narrow black stripe bordering proximally the silvery area of E^3 they evidently have totally lost their most typical property of being concentric to the eye-spots and therefore cannot be recognized. The assumption is more plausible that the distal halves of the Circuli have vanished at all which is in accordance with their beginning atrophy in figs. 233, 234. The described status is essentially the same in the final specimen of our *hero* series (fig. 237). Its characteristic feature however, is that its yellow *iU* area has undergone an expansion as compared to the preceding specimens. The expansion is very considerable which may be illustrated by the fact that in fig. 237 the length of *iU* in the 3rd cell doubles its breadth while in figs. 233, 234 the *iU* shape is but slightly deviating from that of a circle. The indicated expansion shows no dependence upon the eye-spots, the latter being nearly equally sized in all the specimen of our *hero* series, and should be ascribed to the alteration of the *iU* interspace itself. The latter is apparently acting upon the adjacent components, as the shape of *pC* crescents in fig. 237 gives the impression of their being distended by some basipetally directed force. Evidently the expansion of the *iU* interspace is responsible for the latter effect. This is not the first example of the action of the interspaces of the ground color on the pattern components. Another fact of the same phenomenon has been described by me in *Melanargia* (1931, p. 365) in which, however, the active interspace is other than in *Coenonympha* and the result of its activity is also of a different sort. To complete the description of the *hero* evolution it should be remarked that the above symbol *iU* is not quite adequate for the last members of our morphological series. Its meaning—intra-Umbral—suits well fig. 234 where the interspace in question is everywhere surrounded by the derivatives of the Umbra, i.e., by the dissociated Circuli (*dC, pC*). The case is different in figs. 236, 237 where, as we have seen, there is no reason to suppose the existence of

the distal halves of the Circuli (*dC*) so that the interspace marked *iU* is bordered by an Umbral derivative (*pC*) only proximally while its distal border is composed of the third Externa. Accordingly the interspace in question should be designated $E^3 : pC$ in the last *hero* specimens. I have not introduced the latter symbol in the above description as not to overshadow the homologous interrelations and not to complicate the text unnecessarily. But essentially the use of this symbol would be quite correct.

The above described fusion of the Circuli with the third Externa shows somewhat different form in *Coenonympha arcania*. In one specimen of it (fig. 238) none of the Circuli (*C*) shows contact with the third Externa (E^3). In another specimen (fig. 239) the Circuli in the 1st and 4th cells adhere E^3, those in the 2nd and 3rd ones do not. Meanwhile in *hero* no great differences exist between the individual Circuli concerning their distances from the third Externa. It seems that in *hero* the ocellar series together with the Circuli is more flexible than in *arcania*, and in the latter some rigidity is apparently present in it. Therefore the total of the component in question is rather exactly concentric with the third Externa in the former species, not being so in the latter. Similar rigidity of the ocellar series has been also recorded by me in *Melanargia* (1931, p. 397).

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§ 3. INDEPENDENCE OF THE CIRCULI FROM THE VENATION.

In fig. 240 which represents a part of the hindwing of *Coenonympha oedippus* there are seen three well pronounced Circuli ($C3$, $C4$, $C5$) which are placed in the respective cells and show no contacts with each other. In another specimen of *oedippus* (fig. 241) the three Circuli have coalasced with each other owing to their expansion. The same is the case of a still another *oedippus* specimen (fig. 242) in which the indicated expansion is more pronounced and respectively the coalescence is broader. The line of the coalescence of $C3$ and $C4$ is that of the dividing vein i.e. the 4th one. That is clear from the fact that e.g. in fig. 241 the two denticles marking the indicated line lie both exactly on the 4th vein. The same is seen in fig. 242. Different is the case of $C4$ and $C5$. Two denticles mark again the line of the coalescence of the last named Circuli. In fig. 241 the proximal denticle lies on the 5th vein, thus the proximal halves of $C4$ and $C5$ being totally placed in the 4th and 5th cells respectively. But the distal denticle lies somewhere anteriorly from the 5th vein so that the distal half of $C4$ crosses over this vein and is partly situated in the 5th cell. Thus evidently the line of the coalescence of the two anterior Circuli and the direction of the 5th vein are not congruent. They form an acute angle, the summit of which lies on the 5th vein at the proximal denticle formed by $C4$ and $C5$.

A further development of the above process is seen in fig. 242. The distal

denticle between $C4$ and $C5$ shows nearly the same position as in the preceding specimen being, however, shifted a little more anteriorly. But the most interesting is the proximal denticle which has left its previous position on the 5th vein and is now situated in the anterior part of the 4th cell. Owing to a more complete fusion of the Circuli the denticle is somewhat blunted but is nevertheless well discernible. The result is that in fig. 242 the proximal half of $C5$ has entered the 4th cell while, as we have already seen, the distal half of $C4$ has entered the 5th cell. Thus an imaginary line connecting the two denticles in question, i.e. that of the actual coalescence of $C4$ and $C5$, crosses over the 5th vein. If being drawn on the figure that line and the 5th vein would form an x-like design.

Exactly the same final condition is reached as a result of somewhat different process in *Coenonympha amaryllis*. In one specimen of it (fig. 243) the fore end of $C4$ has entered the 5th cell, while the hind end of $C5$ is placed in the 4th one, thus both Circuli crossing the 5th vein over. The components in question are separate though the line of their impending coalescence is readily seen in the form of darkish diluted line intersecting the 5th vein. In the next specimen (fig. 244) the two Circuli have fused with each other and accordingly two denticles have arisen marking the line of coalescence: the proximal lying backwards from the 5th vein and the distal which is anterior to the same vein. The state of the things resulted in is the same as in the last *oedippus* specimen (fig. 242).

The Circuli-like eye-spots are typically "cellular" components i.e. their arrangement and other characters are most strongly influenced by that of the cells and veins. When the neighbouring Circuli undergo coalescence the typical case is that the limits of the individual Circuli pass along the corresponding veins and thus the dependence of the pattern components upon the wing venation is revealed in a very clear form. This we have just seen in the interrelations between $C3$ and $C4$ in figs. 240—242, the same may be seen in many other cases as e.g. in the forewing Circuli in figs. 230, 231. But the above data clearly show that this is not an absolute rule, and that the limits between the Circuli belonging to definite cells and the cells themselves may be partly incongruent. Similar incongruities have been met in other genera both in the Circuli and in other components too (SCHWANWITSCH 1930 a, p. 259). The facts of this sort and also some other data recorded in my paper on *Melanargia* (1931, p. 397) support the assumption already made in my previous publications that the wing-venation and the wing-pattern represent two systems essentially, though not wholly, independent from each other. For obtaining a correct idea about the nature of the wing-pattern comparatively few cases of the above independence are perhaps more important than the innumerable examples of the closest pattern components' dependence upon the wing-venation.

§ 4. EYE-SPOTS.

In the present paragraph we will consider a peculiar case of the dislocation of eye-spots in *Coenonympha* and the ways of their elimination resulting in the ocellar formulae typical of the genus.

A. Dislocation.

In *Coenonympha arcanioides* (fig. 245) there is a regular series of eye-spots. Most of them are situated in the broad Umbra (*U*), that of the 6th cell is lying proximally from the Umbra and only its Circulus (*C6*) is in contact with the latter.

In *Coenonympha arcania* (fig. 246) the 6th eye-spot is considerably larger than the others and its Circulus (*C6*) shows contacts with both the Umbra and first Media (M^1) while in the preceding specimen a rather wide area of white background divides the last named stripe from *C6*.

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In another *arcania* specimen (fig. 247) the 6th eye-spot and its Circulus (*C6*) have entered much deeper into the dark cis-Medial area i.e. that proximal to M^1, and every trace is lost of the connection between *C6* and the degenerating Umbra.

Thus in the three above specimens of *Coenonympha* the 6th eye-spot has migrated from the Umbral area into the cis-Medial one. In the next *Coenonympha arcania* (fig. 248) the indicated migration is still more pronounced which is obvious from the fact that the interspace between the eye-spot in question and that lying in the 5th cell has markedly increased, and surpasses greatly the small distances between the numerous posterior eye-spots. The ocellar series has thus divided into two parts, one consisting of the 6th eye-spot only, another built of five eye-spots occupying the cells from number 1 to 5.

A very similar condition is observed in *Coenonympha dorus* (fig. 249). Its 6th eye-spot is divided by the broad interspace from the 5th one while the latter together with the four more posterior ones form a continuous "crowded up" series. The latter, however, shows some distinction from the condition observed in the *arcania* specimens. In figs. 246—248 the interspaces between the eye-spots and the argentated third Externa (E^3) are almost equally narrow in all the cells from the 1st to 5th. In fig. 249 the indicated interspaces are narrow only in the 4th, 5th and also in the 1st cells, while in the 2nd and particularly in the 3rd cells they are markedly wider.

In the next *dorus* specimen (fig. 250) the described relations are more pronounced, viz., the 4th eye-spot has approximated to the third Externa while the 3rd one has discolated basipetally with the result that the distance

between the two indicated eye-spots is wider than that e.g. between the 3rd and 2nd ones.

This distance shows a further increase in the next *dorus* (fig. 251) which is due to the advancement of the basifugal and basipetal dislocations of the 4th and 3rd eye-spots respectively. The 5th eye-spot dislocates together with the 4th one, that is why the distance between it and the 6th eye-spot has increased very considerably compared to the preceding specimen. The most interesting feature of the posterior part of the ocellar series is that the three eye-spots composing it are situated all along an exactly right line which in the three described *dorus* specimens revolves as a whole round some point near its hind end and the result is that the 1st eye-spot dislocates a little basifugally while the 3rd one does the same basipetally. The general result of the above modifications is that the ocellar series of *Coenonympha dorus* is divided into three parts: the just described posterior one, the middle one consisting of a pair of eye-spots closely approximated to E^3 in the 4th and 5th cells and the anterior one consisting of the 6th eye-spot which lies in the level of the rectilinear M^1.

The last specimen of our *dorus* series (fig. 252) exhibits the above interrelations in a still clearer form which is due to the fact that its eye-spots are of a much smaller size than those of the preceding specimens. If not having the latter at the disposal, and examining fig. 252 alone, the assumption could be made that the six eye-spots seen in it represent remnants of three parallel ocellar series. It would be thus supposed that from the most distal series only the 4th and 5th eye-spots are left, the rest being vanished, that the middle series is represented by the 1st, 2nd and 3rd eye-spots (though the 1st one could belong to the distal series as well), and that the 6th eye-spot is the only remnant left of the proximal series. It is evident that there is is room enough on the wing to place all the disappeared members of the three would-be series. The above evidence, however, shows that the hypothesis about three ocellar series is absolutely incompatible with the facts, and the only reason why I have dealt it with is to demonstrate as clearly as possible how strong is the modification which the prototypical series of eye-spots undergoes in *Coenonympha dorus*.

To complete the description of the ocellar series of *dorus* a fact of quite different category should be discussed than those treated in the foregoing.

In fig. 250 the 5th Circulus ($C5$) and the eye-spot circumscribed by it are shaped as regularly circular as in the prototype and the distal half of the Circulus is as well pronounced as the proximal one. In the next figure that distal half does not exist as independent component being totally coalesced with the dark brim of the argentated E^3. The outline of the said half may be, however, easily restored on the basis of the shape of the yellow interspace dividing $C5$ from its eye-spot. It is evident that the distal half of $C5$

is flattened while its proximal half retains typically semicircular form. The same flattening though in a lesser degree is conspicuous in the distal half of the 5th eye-spot itself. The most plausible "explanation" of this is that the 5th Circulus and eye-spot are pressed by some basifugally directed force against the third Externa and the above described flattening of them is resulted in. The difficulty, however, is that if the hypothesis is apparently suitable for the Circulus, which adheres the third Externa and even fuses with it, it does not seem adequate for the eye-spot which shows no contacts whatever being wholly surrounded by the above mentioned yellow intra-Circular zone, unless we suppose that the latter underlie the action of the above hypothetical force in the same degree as the dark prototypical components. Whatever the forces governing the wing-pattern mechanism may be it is evident that by the given case the phenomenon of the interaction of pattern components is exemplified. Several forms of it are recorded in my previous publications not to be enumerated here. I want only to refer to one example because of its close resemblance to the present case (128, p. 511). In the South American Satyrid *Callitaera polita* the 5th hindwing eye-spot and its Circulus are flattened as if being pressed against the termen (text-fig. 7). The only difference between the *Coenonympha* and *Callitaera* cases that instead of the third Externa in the former, the wing-margin serves one of the factors of the flattening of eye-spot in the latter.

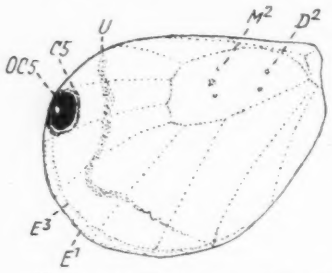

Fig. 7. Flattening of the 5th eye-spot (*OC*5) in *Callitaera polita* due as it were to its being pressed against the wing-margin. *C*5 fifth Circulus, other letters as in text-fig. 2. (SCHWANWITSCH, 1928.)

B. Erebisation.

We have seen that erebisation is recorded in *Satyrus, Oeneis, Parargc, Epinephele, Aphantopus* and *Erebia. Coenonympha pamphilus* v. *lyllus* (fig. 256) represents one of the good examples of the modification, for its large 5th eye-spot is markedly dislocated basipetally compared to the undislocated place of the vanished 4th one which place is indicated by the light intra-Umbral circle lying in 4th cell. Consequently *Coenonympha* may be added to the above enumerated genera and thus out of nine palaearctic genera dealt with in the present series of papers there are only two, viz., *Melanargia* and *Triphysa* in which no examples of erebisation have been discovered. It should be pointed out, however, that the tendency of erebisation in spite of its clear manifestation cannot be called strong in *Coenonympha*. While e.g. in *Erebia* it seems impossible to find a specimen

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with a sufficiently developed ocellar series in which no trace of erebisation would be present, there is a number of patterns in *Coenonympha* which exhibit no inclination whatever to erebisation. E.g., in figs. 276, 286 the 5th forewing eye-spot is not in a slightest degree dislocated in any direction compared to the 4th and 6th ones, thus the ocellar series being of quite prototypical character in the indicated specimens belonging to different species of the genus. Consequently erebisation belongs to widespread intergeneric tendencies but different genera vary greatly as to the degree of its manifestation.

C. Combinations.

Elimination of definite eye-spots and the resultant characteristic combinations of the remaining ones is one of the commonest ways of the modifications of the ocellar series.

E.g. in *Coenonympha leander* and *Coenonympha symphyta* (figs. 253, 254) only the 5th eye-spot is present on the forewings while the hindwings exhibit very polynome series the total being expressed by the formula

$$\frac{OC\ (— — — — 5. — — —)}{OC\ (1.\ 2.\ 3.\ 4.\ 5.\ 6. —)}.$$

Coenonympha nolckeni (fig. 255) shows the same composition of its hindwing ocellar series while no eye-spots at all are present on the forewing the total of the ocellar series being $\frac{OC\ (— — — — — — — — — —)}{OC\ (1.\ 2.\ 3.\ 4.\ 5.\ 6. —)}$. The ocellar series of this type i.e. multiocellar hindwing and the preponderance of the 5th or of the 4th and 5th eye-spots on the forewing are rather common in *Melanargia, Pararge, Epinephele.*

Another direction in the evolution of the ocellar series viz. the stability of the 2nd and 5th eye-spots on the forewings so typical of *Satyrus* (SCHWANWITSCH, 1929, p. 584) and *Epinephele* also occurs in *Coenonympha* and may be exemplified by *C. hero* (fig. 257). Also the uncommon combination of the presence on the forewing of the 2nd eye-spot alone recorded in *Oeneis* (ibid. p. 631) has been met in *Coenonympha oedippus* (fig. 258).

But besides of the inclination to oligonome series on the forewing which is fairly (cf. figs. 218, 223, 224, 225, 290, 293, 295) there are manifestations of just an opposite tendency namely that to multiocellate forewings. *Coenonympha amaryllis* (figs. 275—279) and *C. oedippus* (figs. 284—288) show it at its best. The ocellar formula of the former species based on figs. 276, 281 is $\frac{OC\ (— 2.\ 3.\ 4.\ 5.\ 6. — —)}{OC\ (1.\ 2.\ 3.\ 4.\ 5.\ 6. —)}$ that of the latter $\frac{OC\ (1.\ 2.\ 3.\ 4.\ 5. — — —)}{OC\ (1.\ 2.\ 3.\ 4.\ 5.\ 6. —)}$.

Both formulae are very complete and with regard to the tendency which they express *Coenonympha* resembles some other genera also often exhibiting multiocellate conditions as e.g. *Oeneis* and *Erebia*.

§ 5. FIRST MEDIA.

Like many other genera *Coenonympha* shows a great variety of modifications in its first Mediae.

A. Coenonymphoid dislocation.

In *Satyrus* which occurs in *Pararge* too (p. 158) I have described a modification in the hindwing first Media called coenonymphoid (1929, p. 599). Let us examine now its development in the genus which it derives the name from.

Two specimens of *Coenonympha pamphilus* v. *lyllus* exhibit a more or less prototypical status in the first Media (M^1). In one of them (fig. 259) M^1 shows in general a prototypical habitus but owing to the great length of the discal cell the end of the latter pierces the stripe as it were. Because in another specimen (fig. 260) the cell portions of M^1 are very convex the stripe looks less prototypical than in fig. 259. But the end of the discal cell lies rather far from the main direction of the stripe.

In another *lyllus* (fig. 261) the cell portions of M^1 are convex like the preceding specimen but the stripe has dislocated basipetally in the 3rd and in the posterior part of the 4th cell so that the summit of the discal cell is situated a little distally from the dislocated portions thus resembling fig. 259 in a way.

In the next *lyllus* (fig. 262) the above dislocation of M^1 has advanced. The stripe has totally disappeared from the 3rd cell while in the preceding specimen it is represented there by a tiny marking. Meanwhile in the discal cell there is an undoubted portion of M^1 which shows all the typical characters of the stripe in question, viz., it represents an accumulation of dark pigment dividing the two differently colored areas — distal which is very light and proximal which is only a little lighter than the stripe itself. Exactly the same distribution of colors is seen in every cell crossed by the first Media. Thus obviously the latter has entered the discal cell though at a small extent.

In the next *lyllus* (fig. 263) the light area in the summit of the discal cell shows a marked expansion as compared to fig. 262, i.e. the first Media has advanced further in its basipetal dislocation.

A still further advance of the dislocation is seen in the next *lyllus* (fig. 264) in which the light area in the summit of the discal cell instead of being triangular as in fig. 263 is fork-shaped, the two branches of the fork

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extending along the discal and median veins. This specimen is, however, not sufficiently typical as in the discal cell the first Media has lost its dark pigment and does not differ in color from the wide Medio-basal area which is not the case in all other cells.

Finally *Coenonympha thyrsis* (fig. 265) shows the maximum development of the modification. The discal portion of M^1 is considerably darker than the Medio-basal area bordered by it and the interspace between it and the veins forming the apex of the discal cell is wider than in any preceding specimen.

Thus it is evident that the portions of the first Media primarily situated in the 3rd and in the posterior part of the 4th cells gradually migrate into the discal cell and come to lie rather far proximally from the apex of the latter. Because the neighbouring portions of M^1 remain more or less stationary the general course of the stripe becomes strongly bent inwards on the level with the discal cell. That general concavity is particularly pronounced in fig. 264. Now it is interesting to compare immediately fig. 260 with fig. 265. In the former M^1 is present in the 3rd cell and on the total extent of the 4th one. In the latter no 3rd portion of M^1 is existing which has evidently entered the discal cell. But also the posterior half of the 4th M^1 cell-portion is absent which should be also looked for in the discal cell. Now the emphasis should be laid upon the fact that the short convex portion of M^1 lying in the discal cell is quite continuous and shows no subdivision. Consequently the two portions of the first Media which represent two more or less independent components in figure 260 have totally amalgamated and formed a single component after they have left their cells and migrated into the discal one. In other words a given part of the first Media may consist of two or only one portion according to the number of cells crossed by it, and by this a closed dependence of the form of stripe is demonstrated upon the wing-venation. It is noteworthy that in the Circuli of *Coenonympha* we have seen the manifestation of just opposite tendency, i.e., that of the independence of pattern components from the nervures. This should not be regarded as a contradiction; one only has to borne in mind that the wing-pattern is an extremely complicate phenomenon, and that numerous tendencies of very different directions are at work in its evolution.

In *Coenonympha arcania* (figs. 266—270) the above described modification shows somewhat different form. The main difference between the first Mediae of *lyllus* and *arcania* is that in the former the component is in the condition of a typical stripe, while in the latter it represents only a boundary of the dark Medio-basal field which is of exactly the same color as the field itself.

In fig. 266 the first Media (M^1) is distal to the discal cell but approaches the latter so closely in the 3rd and 4th cells that the apex of the discal cell almost pierces the stripe.

In fig 267 M^1 has entered the discal cell at a small extent so that a narrow zone of white has appeared between the component and the short nervure closing the 3rd cell. In fig. 268 owing to a further basipetal dislocation of M^1 the indicated zone has transformed into a rather wide light area. In fig. 269 the latter has markedly expanded and represents an elongated triangle. Finally in fig. 270 the white area not being so long as in the preceding specimen is, however, much broader and the direction of the intradiscal M^1 portion bordering the area in question is mainly transverse to the cell. Thus evidently the first Media in *Coenonympha arcania* has undergone basipetal dislocation in its middle part and owing to this has crossed over the discal veins and entered the discal cell. The process is essentially the same as in the above described *thyrsis* case but the extent of the dislocation is greater in *arcania*.

As it has been mentioned the coenonymphoid dislocation of the first Media has been recorded by me in *Satyrus* and *Pararge*. With regard to it the former genus differs but slightly from *Coenonympha* though the dislocation in it is of a much more restricted scale (1929, p. 599). In *Pararge* owing to the comparatively short discal cell the dislocating Media does not enter the latter.

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B. Tongue-like protrusion.

In *Coenonympha corinna* (fig. 271) the first Media (M^1) shows a rather prototypical course with the exception of its 4th and 5th cell-portions which are strongly dislocated basifugally and form a peculiar tongue-like protrusion. In another *corinna* (fig. 272) the described protrusion is still more pronounced, and in a still another (fig. 273) its distal end has nearly reached the eye-spot lying in the 5th cell and the "tongue" itself has become very long. It should be emphasized that in the 3rd cell M^1 shows no inclination to leave its initial position. On the other hand the Umbra (U) shows a maked increase in fig. 273 that is why the interspace $U:M^1$ which is so wide in fig 271 has become so narrow and sinuous in fig. 273. Because besides this the Umbra has fused in several places with the strangely dislocated M^1 portions the general aspect of the last *corinna* specimen is very peculiar.

C. Oblique dislocation.

Oblique position of the first Media on the forewing is one of the most common modifications of this stripe and has been recorded by me in several

genera of palaearctic Satyridae. *Coenonympha thyrsis* (fig. 274) exemplifies the modification in the genus under consideration. Its almost rectilinear M^1 and the termen form a considerable angle, so that the hind end of the stripe points exactly to the tornus. The prototypical condition of M^1 parallel to the termen and directed by its hind end far proximally from the tornus may be seen e.g. in fig. 275.

D. Atrophy.

The modification to be dealt with in the present section takes place on both wings of *Coenonympha amaryllis*. Because, however, its development on the forewing shows a form somewhat different from that on the hind one we will consider the two wings separately.

Let us begin with the forewing. In fig. 275 well pronounced Umbra and first Media (U, M^1) are seen which are divided by a light Umbro-Medial interspace. In fig. 276 the indicated interspace has darkened so that the area distal to M^1 and that proximal to it are both of the same color. The stripe itself is, however, clearly visible. In the next specimen (fig. 277) it has become considerably fainter, shows degeneration in the 5th cell and has totally disappeared from the 6th one. In fig. 278 the degeneration of M^1 is still more pronounced, the stripe has become so light that it differs but slightly from the background. Finally in the last specimen of the series (forewing in fig. 279) no trace of M^1 is present. Thus the first Media totally disappears from the forewing of *amaryllis* by the way of a gradual lightening.

In the hindwing of *Coenonympha amaryllis* represented in fig. 280 we see the first Media (M^1), the Umbra (U) which is partly transformed into the Circuli surrounding the pronounced eye-spots and the Umbro-Medial interspace ($U:M^1$) between the two first named components. In the next *amaryllis* specimen (fig. 281) the Umbra has somewhat widened and has touched M^1 in the 2nd and 3rd cells. Owing to this the Umbro-Medial interspace has dissolved into anterior ($U:M^1$) and posterior ($U:M^1$1) portions; the fact should be emphasized, however, that notwithstanding the indicated contact M^1 still exists in all the cells in which it is present in the preceding specimen. This is not so in the next *amaryllis* (fig. 282) where M^1 has vanished from the 2nd and 5th cells, and the anterior portion of the Umbro-Medial interspace is restricted to the 4th cell alone ($U:M^1$4). In the next specimen of *amaryllis* (fig. 283) the first Media has disappeared also from the 1st and 3rd cells which show pronounced portions of the component in fig. 282. Accordingly the $U:M^1$1 interspace has also disappeared, and the result is that the only remnants of the first Media and Umbro-Medial interspace are those lying in the 4th cell ($M^1$4, $U:M^1$4). It is noteworthy that the direction of $M^1$4 is not transverse but very oblique, the

anterior end of the component being strongly dislocated in the basifugal direction; an obvious tendency of $M^1 4$ to this position is easily seen in fig. 282 as well. The final specimen of our *amaryllis* series (fig. 279) does not differ substantially from fig. 283 with regard to its hindwing; but on comparing it to figs. 275 and 280 the extent of the evolutionary process becomes particularly obvious; the long stripe M^1 and the wide interspace $U : M^1$ disappear totally from the forewing and the small vestiges $M^1 4$ and $U : M^1 4$ are their only remnants on the hind one. The fact should be emphasized now that the just described evolution of *amaryllis* pattern is extremely typical of the genus *Coenonympha* in general. The white triangular marking $U : M^1 4$ on the hindwing belongs to the most constant characters of a number of *Coenonympha* forms. It may be seen e.g. in fig. 294 and has been met with also in some *Pararge* (fig. 56) and *Erebia* (figs. 161—163).

E. Fusion with the Circuli.

Coenonympha oedippus (figs. 284—289) shows sowewhat different way of the disappearance of the first Media than that of *amaryllis* described in the preceding section.

Let us begin with the forewing. In fig. 284 the first Media (M^1) and the pronounced Circuli (C) are divided from each other by a light wide Umbro-Medial interspace ($U : M^1$). Though no typical diffused Umbra is present in this *oedippus* specimen it is natural to call the interspace Umbro-Medial as the Circuli derive from the Umbra.

On the forewing of the next *oedippus* specimen (fig. 285) the indicated interspace has markedly darkened and somewhat narrowed so that M^1 lies nearer to C than in the preceding figure. On the forewing of the next specimen (fig. 286) the interspace $U : M^1$ has become still darker and still narrower so that the distance between M^1 and C is quite short. Besides this M^1 is less intensely pigmented than in the preceding figure. On the forewing of a still another *oedippus* specimen (fig. 287) M^1 has come to lie very near by the line of Circuli (C). In the 2nd and 3rd cells very narrow slit-like remnants of the $U : M^1$ interspace still exist between M^1 and C. But near the veins the strongly curved M^1 cell-portions have already fused with C and accordingly the $U : M^1$ interspace of the 2nd cell has separated from that of the 3rd one. The interspaces in question are not designated by indexes in the figure as owing to their being very narrow the pointing lines would make the interrelations existing in the pattern not clear enough; on comparing the specimen with fig. 286 it is easy, however, to find the interspaces. In the 4th cell no vestige of the $U : M^1$ interspace is present and the M^1 portion has fused with the corresponding portion of C. The M^1 portion itself is, however, quite rudimentary and represents but a shadow-like outgrowth

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of *C*. The homologisation is nevertheless quite unquestionable as similar outgrowths are seen on proximal sides of M^1 cell-portions in the 2nd and 3rd cells. In the 5th cell no trace of M^1 is existing while *C* is sufficiently pronounced. Owing to a somewhat darker coloration of *C* compared to M^1 the described interrelations are easy to see. Thus evidently M^1 disappears not by the way of simple atrophy in loco as we have seen it in *amaryllis* but the degenerating stripe approaches to and fuses with the Circuli.

Let us now pass on to the hindwings of the above described *oedippus* specimens. In fig 284 the hindwing shows light wide $U:M^3$, pronounced M^1 and typical *C*. In another specimen (fig. 285) $U:M^1$ is little narrower, in a still another (fig. 286) it is considerably narrower so that M^1 has approached *C* very closely especially on the 2nd and 3rd veins where the first named stripe forms prominent denticles. In the next specimen (fig. 287) the denticles of M^1 and the portions of *C* are in contact or nearly so. Therefore the narrowed white $U:M^1$ intespace continuous in fig. 286 has subdivided into three fragments in fig. 287. In the specimen of *oedippus* represented in fig. 288 the hindwing shows somewhat different interrelations. Its M^1 cell-portions have become crescent-like and exactly concentric to the portions of *C* which is not the case in the preceding specimen with its angular M^1. Owing to this the remnant of the $U:M^1$ interspace between M^1 and *C* is more or less uninterrupted and shows in its whole extent nearly the same breadth. That breadth is, however, very minute owing to the close approximation of M^1 to *C*. Besides all this M^1 is considerably lighter than in the preceding specimens; its lightening is very advanced in the 1st cell where the stripe is hardly visible while in the 5th one the process has resulted in the total disappearance of the component. Finally in fig. 289 no remnants of M^1 are visible on the hindwing and the same is the case on the forewing.

Thus the disappearance of the first Media from the wings of *Coenonympha oedippus* is a complicated modification consisting of several process. The first and perhaps the most important of them is the basifugal dislocation of the stripe and its closest approximation to the Circuli. Undoubted fusion of the two components takes place in the 4th forewing cell in fig. 287 and near the 3rd veins of both wings of the same specimen. It is noteworthy that the dislocation is the most pronounced in the veinous parts of M^1, and therefore the indicated fusion begins near the veins while the interveinous areas mostly do not show coalescence yet. Another process is the lightening of M^1 which is seemingly the principal factor of the disappearance of the stripe. It is interesting that the closely situated *C* seems not to be affected by this process which is illustrated by the forewing in fig. 287 and by the hind one in fig. 288. The third process is that of the darkening of the Umbro-Medial interspace. It is better pronounced on the forewing than on the hind one, as the latter shows still nothing of it in fig. 287 where the interspace has already

become quite narrow, and only in fig. 288 the hindwing shows darkening in the extremely narrow interspace between C and M^1. It should be pointed out that the darkening of the $U:M^1$ may be quite independent from both lightening of M^1 and its basifugal dislocation. E.g. in fig. 288 none of the two latter processus is much pronounced on the forewing but its $U:M^1$ is dark.

On comparing now the *oedippus* evolution (figs. 284—289) with that of *amaryllis* (figs. 275—283) it should be pointed out that there are both resemblances and distinctions between the two species. The resemblances are that in both species M^1 undergoes lightening while $U:M^1$ becomes dark. But while in *amaryllis* M^1 vanishes in loco, in *oedippus* it shows typical basifugal dislocation. Another distinction is that in *oedippus* M^1 disappears totally while in *amaryllis* a portion of the stripe and of the Umbro-Medial interspace remain in the hindwing ($M^1 4$, $U:M^1 4$).

With the exception of the latter difference the final results of the evolution of the two species (figs. 279 and 289) are rather similar: in both of them the wing-pattern principally consists of the silvery third Externa (E^3) and the series of pupillated encircled eye-spots, while the greater area of both wings proximal to the last named components is quite empty (fig. 289) or nearly so (fig. 279).

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CHAPTER XIII.

PRINCIPAL TYPES OF THE UNDERSIDE IN COENONYMPHA.

In the preceding chapter we have seen which are the modifications of the prototype in the individual components of *Coenonympha* underside pattern. In the present chapter we will consider several undersides typical of the genus taking each of them as a whole while in the last paragraph a few remarks will be made about the upperside and its relation to the underside.

§ 1. OCELLATE AND UMBRO-MEDIAL PATTERNS.

In one of the paragraphs of the preceding chapter we have seen how numerous and well pronounced are the eye-spots in *Coenonympha*. We have now only to point out that in many forms of the genus the ocellar series plays a dominating rôle. This is the case of figs. 253 and 255 in which the third Externa on the hindwing (E^3) is the only stripe present, while in fig. 254 even this is absent. The *Coenonympha amaryllis* and *oedippus* specimens

represented in figs. 279, 289 resp. also belong to the ocellate type notwithstanding the stripes being better developed in them than in the three above forms.

In several palaearctic genera of Satyridae dealt with in my publications a particular type of the underside, and also of the upperside, has been described termed Umbro-Medial. By this the cases are meant when the Umbro-Medial interspace is more or less wide and light. This type of pattern occurs on *Coenonympha* too and we have to consider two examples of it.

One of them is *Coenonympha arcania* v. *marginalis* (fig. 290). The Umbro-Medial pattern exists on its hindwing only where the broad suffused Umbra (U), pronounced first Media (M^1) and white interspace between them ($U:M^1$) are so characteristic that any further comment seems unnecessary. On the forewing the first Media is undergoing a marked atrophy owing to its becoming as ochreous yellow as the greater proportion of the wing area and thus there is no Umbro-Medial pattern on the forewing.

It is very interesting that the above condition greatly resembles a pattern occuring in that of *Epinephele pasiphaë* (fig. 94). The most characteristic features of both patterns under comparison are: (1) On the forewing the degeneration of M^1 and U, strong development of the 5th eye-spot, absence of the remaining ones and yellow coloration of the great proportion of the wing except its peripheric zone. (2) On the hindwing typical $U:M^1$ interspace, polynome ocellar series and dark coloration of the wide area between M^1 and the basis of the wing. There are also distinctions principally concerning Externae. But they affect neither the homologous resemblance of the two forms, nor their similar appearance. Undoubtedly this is an example of parallelism which is especially noteworthy owing to the fact that the two species are of quite different size, *Epinephele* being a much larger butterfly than the small *Coenonympha*.

Another example of Umbro-Medial pattern is *Coenonympha hero* (fig. 291) which differs from the preceding form in its much more pronounced eye-spot series. On the forewing the existence of the typical Umbra (U) and no less typical Circuli (C) should be noted, on the hindwing the last named components have dissolved into distal and proximal halves each (dC, pC) which modification is already described in the foregoing. The Umbro-Medial interspace ($U:M^1$) is very outstanding and colored white. The fact of its being limited partly by the Circuli instead of typical Umbra does not affect its homologisation as the former components derive from the latter. The hindwing $U:M^1$ interspace of *hero* does not deviate essentially from that of *arcania* (fig. 290) but with regard to the forewing a marked difference between the two should be noted. *Hero* shows the same color-pattern on

both wings, and accordingly its forewing $U:M^1$ is quite similar to that of the hindwing, while in *arcania* we have seen the absence of $U:M^1$ on the forewing owing to the quite different color-pattern type of the latter. The described interrelations of the two species just fall under the two types of the OUDEMANS' phenomenon, the manifestation of which in the genus *Coenonympha* will be discussed in the chapter XVII.

Coenonympha hero deserves, however, some more attention with regard to its coloration. The $U:M^1$ interspace and pupils are white in fig. 291, while the Ocello-Circular, or to say simpler, intra-Umbral rings (iU) are yellow, which difference is readily seen even in our monochrome drawing. The indicated distribution of colors is extremely typical not only of Satyrids but also of the Nymphaloid families in general when yellow and white are present together in a wing. Among palaearctic Satyridae another good example of this is *Erebia turanica* (fig. 182).

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§ 2. IPHIS PATTERN.

By this paragraph we begin the description of four *Coenonympha* undersides which are selected from the genus as most typical of it and interesting from the morphological point of view.

The wing-pattern of *Coenonympha iphis* (figs. 292—294) is one of the best known and its main characters are present in some other *Coenonympha* species too as e.g. *C. pamphilus* or *C. tiphon*. The analysis of the *iphis* specimen represented in fig. 292 is very simple. There are first Externa on the forewing (E^1) and silvery third Externa on the hind one (E^3) which are followed by the broad Umbra (U) on both wings and series of eye-spots on the hindwing. The white Umbro-Medial interspace ($U:M^1$) particularly wide on the hindwing passes between the Umbra and first Media (M^1), the latter component forming the limit of the wide dark area extending to the wing basis and exhibiting no other components.

In the hindwing of the next *iphis* specimen (fig. 293) the Umbra and first Media coalesce in the 2nd cell owing to the broadening of the first named component, and thus the Umbro-Medial interspace becomes divided into the short posterior ($U:M^1 1$) and longer anterior ($U:M^1$) portions. On the forewing the posterior end of $U:M^1$ has disappeared owing to a similar process of fusion.

In the last *iphis* specimen (fig. 294) nothing is left of $U:M^1$ on the forewing, while on the hindwing the interspace is restricted to the 4th cell only ($U:M^1 4$) the rest being totally vanished as well. On comparing fig. 294 and 293 it is ready to see that in the latter the described disappearance is ripening, as besides the mentioned division of $U:M^1$ into two parts the interspace shows a marked narrowing in the 3rd and 5th cells, while in the 4th one

it remains broad. It should be emphasized that the $U:M^1 4$ remnant of the Umbro-Medial interspace, when formed, proves to be very constant and is not inclined to disappearance; in fig. 294 it represents a well pronounced and very outstanding white marking. The latter undoubtedly belongs to the most typical characters of the genus *Coenonympha* and occurs in a number of its species. Its homologues are seen in *C. sunbecca* (fig. 302) and *C. mongolica* (fig. 305) but the closest resemblance to it exhibits *C. amaryllis* (figs. 283, 279) in which the process of its formation is already referred to (p. 227, figs. 280—283). In both *amaryllis* and *iphis* the triangular shape of the $U:M^1$ marking is very characteristic which is due to the basifugal dislocation of the anterior end of the 4th M^1 cell-portion while the hind end of the latter remains more or less stationary.

Undoubtedly the underside pattern of *Coenonympha iphis* in which no components but the hindwing eye-spots and $U:M^1$ play any noticeable rôle should be regarded as highly specialised. The fact also should be reminded here that a very similar process and resultant pattern takes place in *Pararge roxandra* (fig. 56).

§ 3. SEMENOVI PATTERN.

If in the preceding paragraph we have seen a tendency which is typical not only of the whole of the genus *Coenonympha* but also occurs in other genera, the modification observed in *Coenonympha semenovi* (figs. 295—297) stands rather apart even within the genus *Coenonympha*.

The forewing of *Coenonympha semenovi* with the gradual suppression (figs. 295, 296) and total disappearance (fig. 297) of the $U:M^1$ interspace does not represent anything exceptional. But on the hindving of *semenovi* (fig. 295) four main pecularities should be indicated. (1) No eye-spots are present notwithstanding the fact that the intra-Umbral rings (*iU*) in which they should be placed represent a continuous and well developed series. A singular "eyeless" appearance is resulted in. (2) The Umbra (*U*) forms regular, tongue-shaped, basipetal protrusions in every cell crossed by it. The protrusions in the 2nd and 3rd cells are the largest while those in the 5th and 6th ones have fused with each other. (3) The first Media (M^1) is most peculiarly shaped. It forms four long tongues, the anterior and two posterior ones being located in the 7th, 2nd and 1st cells resp. while the middle one covers two cells, viz., the 4th and 5th ones. The incisure between the latter tongue and that of the 2nd cell is so deep that M^1 enters the discal cell in this area. (4) The coloration of the Medio-basal area is much darker than that of the Umbral zone.

The subsequent evolution of the *semenovi* pattern principally consists of the expansion of the Medio-basal area and the fusion of its tongues with the

Umbra. An undoubted tendency to the fusion is readily seen in fig 295 where the M^1 tongue in the 2nd cell and the corresponding outgrowth of the Umbra are already in contact.

In the next specimen (fig. 296) the indicated contact in the 2nd cell shows some advance, another contact of the same components is ripening in the 4th cell, while in the 1st one the Umbral and Medio-basal areas have widely coalesced. The general extent of the Medio-basal area has markedly increased compared to the preceding specimen and the interspace $U:M^1$ has become narrower.

Fig. 297 shows the completion of the process. The two large tongues of the first Media have reached the Umbra and fused whit it. One of the fusions covers the total of the diameter of the 2nd cell, while another extends over the total of the 5th cell and a considerable proportion of the 4th one. The most anterior tongue of the Media has also reached the Umbra just along the costa, but its significance is less than that of the other two. Owing to the described fusions the Umbro-Medial interspace has divided into three independent portions: a small one lying in the 1st and 2nd cells ($U:M^1 1.2$), a large very curved one in the 3rd and 4th cells ($U:M^1 3.4$) and a cap-shaped one in the 6th and 7th cells ($U:M^1 6.7$).

Finally a considerable darkening is observed in the total length of the Umbra and in the terminal parts of the anterior cells. The impression is born out that the dark coloration has penetrated, as it were, through the above described Medio-Umbral coalescences from the cis-Medial area into more peripheric ones.

The general result of the above processes is that the hindwing of *Coenonympha semenovi* evolves one of the most peculiar patterns occurring in the Nymphaloid families.

§ 4. SUNBECCA PATTERN.

The wing-pattern of *Coenonympha sunbecca* (fig. 300) belongs to the most exquisite "final results" occurring in the genus, and its peculiar character increases owing to its coloration totally devoid of yellow hues so common in *Coenonympha*. Its white background resembles the genus *Melanargia* in a way. Morphologically *sunbecca* pattern reveals some affinities to that of *semenovi*, dealt with in the preceding paragraph, as like the latter it is "eyeless", that is, its large, numerous and regularly shaped intra-Umbral circles (*iU* in figs. 298—303) contain no corresponding eye-spots. Only in a single specimen of *sunbecca* I was able to discover a tiny rudiment of the eye-spot lying in the 6th intra-Umbral circle (*iU*6) of the hindwing (fig. 302).

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A. Forewing.

Let us dwell first on the evolution of the forewing of *sunbecca*. Fig. 298 represents the most prototypical condition discovered in it. There are seen the first and third Externae (E^1, E^3); the latter borders the typical Umbra (U) including a series of pronounced Umbral circles (iU) without eye-spots in them. The first Media (M^1) notwithstanding the absence of its posterior end is typical, which is also the case of the Umbro-Medial interspace ($U:M^1$). A tiny first Discalis is also noteworthy (D^1).

On the forewing of the next *sunbecca* specimen (fig. 299) a pronounced melanisation is observed. Owing to the latter the terminal zone of the wing has so darkened that that E^3 is quite vanishing, while the long subcostal tract between M^1 and the wing basis represents now a continuous dark area in which D^1 has disappeared. The first Media itself has lost its strial character so pronounced in the preceding specimen and serves now but a boundary of the described dark area.

The last forewing in the *sunbecca* series (fig. 300) is melanised nearly in its whole. Only two regular series of white markings cross over it. The distal of them is that of the intra-Umbral circles (iU) the individual markings of which have somewhat decreased compared to the above specimens. The proximal series ($U:M^1$) derives from the division of the continuous Umbro-Medial interspace of the preceding specimens into cell portions.

B. Hindwing.

We begin the analysis of the *sunbecca* hindwing with fig. 301. It shows typical first Externa (E^1), vanishing third Externa (E^3) and a characteristic Umbra (U) which surrounds the intra-Umbral (iU) circles and is followed by the Umbro-Medial interspace ($U:M^1$); the first and second Mediae (M^1, M^2) are typically shaped and placed, and the interspace between them is quite darkened. The basis of the wing exhibits a characteristic basifugal melanisation (Bm). A broad interspace is left between the latter and the second Media in the anterior cells ($M^2:Bm7, M^2:Bm4$), while in the cells posterior to the discal one the two components are fused together and neither M^2 nor any light interspace are existing.

Let us consider now the light marking $iU6+(U:M^16)$ lying in the 6th cell. To get a correct idea of its homologies we have to return to one of the preceding *sunbecca* specimens (fig. 298). There are two white markings in its 6th cell which are divided by a narrow dark stripe from each other. The distal of them is shaped oval ($iU6$), the proximal one shows a less regular shape and is of a very small size ($U:M^16$). The homologies of the two markings are evident from their lettering, and the dividing stripe should be

regarded as a narrowed portion of the Umbra. Passing now again to our initial hindwing we see that the two markings in question independent in fig. 298 have fused together in fig. 301, and thus formed rather a large marking $iU6+(U:M^16)$ which, however, reveals a trace of its origin in the form of a tiny dark denticle subdividing the anterior area of the marking and evidently representing a remnant of the above dividing stripe existing in fig. 298, i.e., of the Umbra. Thus evidently in the 6th cell the Umbro-Medial interspace and intra-Umbral circle fuse together.

This fact being interesting in itself has, however, no bearing on the subsequent evolution of *sunbecca* hindwing. In fig. 299, which we have to examine now, the regular shape of $iU6$ gives no indication of any other component taking part in it, and it seems most likely that the vestigial marking $U:M^16$, still existing in fig. 298, has disappeared in fig. 299, and that no fusion of $iU6$ and $U:M^16$, so evident in fig. 301, takes place in fig. 299. As to the other components seen in fig. 299 a stronger development of the Umbra should be noted in it compared to fig. 301. Owing to this the peripheric zone of the wing now represents a dark background on which a series of fine intra-Umbral markings stands out ($iU1$, $iU6$). The area of basifugal melanisation comparatively small in fig. 301 has increased in fig. 299 with the effect that the light interspaces $M^2:Bm7$ and $M^2:Bm4$ which are nearly in contact in the first named figure have become quite independent in fig. 299. Finally the Umbro-Medial interspace ($U:M^1$) which is not very outstanding in fig. 301 owing to the light coloration of the Umbra (U) has become prominent owing to the darkening of the latter component in fig. 299. Besides this its subdivision into cell-portions should be noted which is principally due to the lengthening of the basifugal protrusions of M^1 along the veins.

In the hindwing of the final specimen of our *sunbecca* series (fig. 300) a further increase in all the dark areas is observed which results in a contraction of all the light interspaces. There are three transverse series of the latter: (1) the intra-Umbral series consisting of half a dozen of almost exact circles (iU, $iU6$); (2) the Umbro-Medial series $U:M^1$ which shows great differences in the size of its individual markings and lacks that of the 6th cell, and (3) the Medio-Basal series consisting of two markings only: one in the discal cell ($M^2:Bm4$), another in the 7th one ($M^2:Bm7$). All the enumerated markings are smaller than their homologues in the preceding specimen, so that the wing might be described as dark with a light pattern. The fact should be finally emphasized that the coloration of the dark areas in fig 300 is nearly the same everywhere, while in fig 301 those proximal to M^1 are much darker than the Umbra.

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C. Comparisons.

It is out of the question that the described wing-pattern of *Coenonympha sunbecca* should be regarded as highly and peculiarly specialised, and without the above analysis its proper homologisation would be hardly possible. If on the forewing with its only two series of undislocated light markings (*iU*, *U*: M^1) the morphological interrelations are comparatively simple, the hindwing is much more difficult for the analysis. There are two principal difficulties in the latter: first that because of the exact position of the *iU*6 marking on the geometrical prolongation of the *U*: M^1 series it seems to belong rather to the latter than to the intra-Umbral one, second that the two Medio-Basal markings (M^2: *Bm*4, M^2: *Bm*7) owing to their being very distant from each other appear to be rather remnants of two parallel series than derivations of one.

In spite of the general appearance of *sunbecca* wing-pattern being very singular it is not unparalleled, in another genus. The underside of *Erebia turanica* (fig. 182) though looking quite differently is nevertheless closely resembling *Coenonympha sunbecca* in the morphological composition of the pattern. The maximum resemblance is observed in the hindwing which like *sunbecca* exhibits exactly the same three series of markings—intra-Umbral (*iU*) devoid of eye-spots, Umbro-Medial (*U*: M^1) composed of irregular spots and Medio-Basal (M^2: *Bm*) consisting of a couple of small markings. Thus the hindwing patterns of the two species are homologous. In the forewing the resemblance is restricted to the intra-Umbral series devoid of eye-spots while no trace of the Umbro-Medial interspaces so prominent in *Coenonympha sunbecca* are present in *Erebia turanica*. There are of course some distinctions between the two species. The most conspicuous of them is coloration. *Erebia turanica* is much heavier melanised than *Coenonympha sunbecca* and looks quite dark. On the other hand its intra-Umbral markings are yellow and the other two series of interspaces white, while in *C. turanica* no trace of yellow is present in the wings and all the interspaces are white. Another distinction is that in the shape of the intra-Umbral series. In the forewing of *E. turanica* the 4th and 5th *iU* markings are displaced basipetally thus serving a good example of the ereboid dislocation so typical of the genus *Erebia*. Meanwhile no ereboid dislocation takes place in *Coenonympha sunbecca*, its intra-Umbral series being undisturbed. A third distinction is that the Medio-Basal series is present in the 1st and absent in the 7th cell of *E. turanica* while just the opposite is the case of *C. sunbecca*. But the described distinctions between the representatives of the two genera are of secondary importance and do not interfere with their fundamental homologous resemblance. The latter is especially remarkable because of the fact that on the basis of the same morphological composition, which is in itself highly spe-

cialised and widely deviating from the prototype, two patterns evolve which owing to a few secondary modifications are extremely dissimilar in their appearance.

§ 5. MONGOLICA PATTERN.

The last underside to be dealt with in the present chapter is that of *Coenonympha mongolica* (figs. 304, 305). Unlike to the preceding *semenovi* and *sunbecca* patterns it is not "eyeless", and the finely developed eye-spots are present in it. A typical first Externa (E^1 in fig. 305), a partly (fig. 304) or wholly (fig. 305) argentated third Externa (E^3) and an atrophying first Media on the forewing (M^1 in fig. 304) are ready to see. A process, however, developing in the 4th and discal cells of the hindwing requires a closer analysis.

To begin with it we have to return again to *Coenonympha sunbecca* pattern described in the preceding paragraph. On the hindwing in fig. 299 the interspace between the 4th cell-portion of the first Media ($M^1 4$) and the discal portion of the second one ($M^2 4$) is rather wide, though narrower than that between the same stripes in the anterior cells. In fig. 303 the indicated interspace has become so narrow that the two Mediae may be considered as practically coalesced in the 4th and discal cells, and it is reasonable to designate them as $M^1 + M^2 4$. The complex component thus evolved represents but a partition between the white areas $U : M^1 4$ and $M^2 : Bm4$. The latter like other interspaces in fig. 303 are rather wide. The wing represented in fig 302 shows a higher degree of melanisation than any figured *sunbecca* specimen, and thus the majority of its white interspaces are much smaller than in fig. 303. This is the case of the interspaces $U : M^1 4$ and $M^2 : Bm4$ as well. But the partition between the latter consisting of $M^1 4$ and $M^2 4$ is considerably broader than in fig. 303. Supposing now the generally small size of white areas existing in fig. 302 and the narrowness of the $M^1 + M^2 4$ partition seen in fig 303 to be combined in one wing the state of the things would be brought to the effect not essentially differing from that of *Coenonympha mongolica* (fig. 304). To obtain a complete resemblance one has only (1) to eliminate from the *sunbecca* specimen represented in fig. 302 its $M^2 : Bm7$ and three vestigial $U : M^1$ markings, (2) to put eye-spots in all its *iU* circles, (3) to add to it a silvery E^3 and (4) to lighten a little its general hue. Thus according to the above derivation the narrow stripe bordering the discal veins in the hindwing of the *mongolica* specimen represented in fig. 304 and resembling the first Discalis of the prototype should be homologised as coalesced portions of the two Mediae ($M^1 + M^2 4$), and the adjacent interspaces, as $U : M^1 4$ and $M^2 Bm4$.

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Supposing now in fig. 304 (1) the $M^1 + M^2 4$ stripe to undergo such a narrowing that its distal margin comes to lie on the discal veins, and (2) $M^2 : Bm4$ to disappear owing to the expansion of the basifugal melanisation attaining the proximal margin of the indicated complex stripe, the condition seen in the next *mongolica* specimen (fig. 305) would be the result. This condition, however, in both its homologies and habitus deviates but slightly from that already seen in *Coenonympha iphis* (fig. 294). In both species the series of pupillated eye-spots and white $U : M^1 4$ markings are the principal constituents of the hindwing pattern. The difference between the two, which is of interest, does not reach the level of homologous distinction, and is restricted to that of the shape of $U : M^1 4$. The latter, however, deserves some attention to be paid to it.

We have seen that in *Coenonympha mongolica* (fig. 305) the proximal border of the white $U : M^1 4$ marking passes along the discal vein and accordingly its fore end is inclined basipetally. This is a natural sequence of the described narrowing of the $M^1 + M^2 4$ complex stripe and of the whole of the evolution of the *sunbecca-mongolica* morphological series referred to. On the contrary in *iphis* (fig. 294) the 4th cell-portion of M^1 has deviated from its original transverse course in an opposite direction, viz., its anterior end is shifted basifugally. This direction is again not a fortuitous one but results from the whole trend of the *iphis* evolution (figs. 292—294) which represents, as we have seen, an interspecific tendency in *Coenonympha*. The main distinction between the evolution of $U : M^1$ marking in the *amaryllis-iphis* series and that in *sunbecca-mongolica* patterns seems to depend upon two different types of the modifications of the first Media. In *sunbecca* the cell-portions of M^1 are markedly concave, and the stripe emits basifugal protrusions along the veins as it is ready to see in figs. 299—301. On the contrary in *iphis* and *amaryllis* the M^1 cell-portions are convex and their veinous points are the most proximal (cf. figs. 292 and 280). The two indicated types of M^1 cell portions may be seen in other *Coenonympha* species too. So, e.g., the convex shape of them is present in *saadi* (fig. 212), *tekkensis* (fig. 219), *dorus* (fig. 249), *lyllus* (fig. 264), *corinna* (fig. 272) and *hero* (fig. 291). The concave M^1 cell-portions are existing in *oedippus* (forewing in fig. 285, hindwing in fig. 286) though in a less pronounced form than in *sunbecca*. In general the convex shape seems to be more common in the M^1 cell-portions of *Coenonympha* than the concave one. Both forms occur in other genera of palaearctic Satyridae too.

To complete the discussion of *mongolica* and *sunbecca* patterns the fact should be emphasized that the narrowing of the $M^1 + M^2 4$ complex stripe is restricted to the 4th and discal cells only, and that its beginning may be seen still in such prototypical Mediae as those in fig. 301. Meanwhile the anterior portions of these stripes do not manifest any tendency to mutual

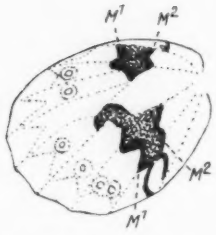

Fig. 8. Hindwing underside of *Melanargia galathea*. Medial band formed by the first and second Mediae (M^1, M^2 resp.) is interrupted in the discal cell. (SCHWANWITSCH, 1931.)

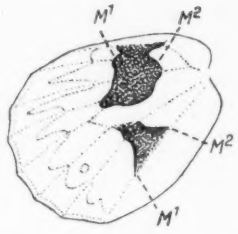

Fig. 9. Hindwing underside of *Satyrus prieuri*. For explanation see fig. 9. (SCHWANWITSCH, 1929.)

approximation, and there are no data at my disposal suggesting the existence of the approximation in posterior cells. This phenomenon again does not stand alone. In the genus *Melanargia* exactly the same process results in an interruption of the Medial band, i.e., of both Mediae (text-fig. 8). A similar modification and interruption take place in *Satyrus* as well (text-fig. 9). There is no actual interruption in *Coenonympha,* but it does not seem unlikely that if in the second specimen of *Coenonympha mongolica* the Umbra and melanisation were less developed and the total extent of the Mediae were not "concealed under them" the same interruption of these stripes would be seen in *Coenonympha* which occurs in *Satyrus* and *Melanargia.*

The upperside patterns of *Coenonympha* will be briefly considered in the chapter XVI together with those of *Triphysa.*

CHAPTER XIV.

REALISATION OF THE NYMPHALOID PROTOTYPE IN THE GENUS TRIPHYSA.

The small genus *Triphysa* Z. comprises according to SEITZ's Palaearctica only one species, that of *phryne* PALL. which is subdivided into five forms. The genus stands somewhat apart in the bulk of palaearctic Satyridae with regard to the general character of its wing-pattern, and some modifications of the prototype occurring in it are of quite a peculiar kind. In spite of this a closer affinity of its wing-patterns to those of *Coenonympha* than to those of any other Satyrid genus seems out of question.

Let us begin with the realisation of the prototype in *Triphysa.* It should be remarked here that because on the one hand there is only one species in the genus and on the other hand the names of the forms which it consists of

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are of secondary importance we will principally restrict ourselves in the below text to the numbers of figures mostly without mentioning specific and forms' names which are all, however, given in the explanation of the figures.

The wings of *Triphysa* represented in fig. 307 show a pronounced silvery third Externa (E^3), a series of eye-spots and a typical first Media (M^1). On account of the data given in the description of *Coenonympha* pattern and of the close affinity between the two genera in question it seems most likely that the second Externa is absent in *Triphysa* while the third one has undergone argentation along the middle line: silvery scales fill up the interspace between the two dark halves of the component thus splitted along. The duplicated condition of the *Triphysa* E^3 is represented at its best in fig. 308, the two black margins of the stripe being of a nearly equal breadth. In our initial specimen (fig. 307) the proximal half of E^3 is heavier than the distal one, and participation of some umbral elements in the former is not unlikely, particularly in the 2nd and 3rd cells of the forewing, so that the condition resulted in should be regarded as more modified than in fig. 308. We have seen in *Coenonympha* some transitionary stages between a more or less prototypical totally dark E^3 and an argentated one. Something like this may be seen in *Triphysa* too. E.g., the two dark stripes and the silvery area between them present in the 2nd and more anterior forewing cells in fig. 307 are replaced by a single dark stripe in the 1st cell. The most plausible explanation is that in the last named cell E^3 is not subdivided while in the remaining ones it has undergone division. Quite the same distinction between the 1st and anterior forewing cells may be seen in fig. 309. Finally in fig. 311 the third Externa represents but a boundary of the dark area proximal to it and shows no silvery coloration in it, thus evidently not having undergone argentation. Thus evidently the behaviour of the third and second Externae in *Triphysa* is the same as in *Coenonympha*. As to the first Externa absent in our initial specimens it may be seen in rather a typical form in figs. 309, 310.

The eye-spots in fig. 307 though minute in their majority are, however, sufficiently typical. A more complete series of them is seen in fig. 309, where the eye-spots in the 1st cells of both wings are present, that in the hindwing being even pupillated while that in the fore one is very tiny. All the other eye-spots in fig. 309 are well pronounced and provided with bright pupils. Their formula is $\frac{OC\ (1.\ 2.\ 3.\ 4.\ 5.\ 6.\ --)}{OC\ (1.\ 2.\ 3.\ 4.\ 5.\ 6.\ -)}$.

The Umbra is not very typical in *Triphysa*. In fig. 310, however, it fills up more or less the interspace between E^3 and M^1, and the characteristic light intra-Umbral rings are left between the component in question and the eye-spots. They are especially pronounced in the 2nd cells of both wings. Still better the same rings are seen in fig 311.

The first Media (M^1) in fig. 307 is sufficiently typical in both the shape and position except the fact of its absence from the 1st forewing cell. But in figs. 313 and 314 the stripe is present in the indicated cell, though being restricted to its anterior part.

The second Media (M^2) in fig. 307 is totally absent in the forewing and shows a very modified condition in the hindwing to be discussed in the subsequent description. But in fig. 312 the discal portion of the stripe in the forewing reveals its prototypical structure though being markedly modified. The stripe is lying close by the discal veins while its hind part is bent basipetally and runs along the median vein, a condition often met in the pierellisation of the second Media. Almost the same status in M^2 is seen in fig. 314. As to the hindwing M^2 the most prototypical condition of the component has been discovered in v. *dohrni* (fig. 315) where it is present in the 7th ($M^2 7$) and discal cells $M^2 4$ a, $M^2 4$ p). Notwithstanding the stripe having undergone a modification to be dealt with in the next section its general status is typical enough to render its homologisation unquestionable. Some indication on the presence of M^2 in the 1st cell of the hindwing may be seen in fig. 324 where the interspace between the two Mediae ($M^1 1, M^2 1$) differs by its light coloration from the general dark background. Its distal and proximal margins exactly correspond with the normal positions of the first and second Mediae in that cell. Thus the presence of the second Media in *Triphysa* is undoubted.

Neither Discalia and Basalia, nor Granulatae have been discovered in *Triphysa*. As to the longitudinal components the white stripes running along the veins in fig. 307 and still better pronounced in figs. 324, 325 correspond in everything with the Venosae of the prototype except their coloration. The latter prevents me like in the case of *Erebia* from considering them as genuine Venosae at least at present when no data are at my disposal which would favour such a comparison.

On the basis of the above the generic formula of *Triphysa* will be the following:

$$\frac{E^1.-E^3.\,OC\ (1.2.3.4.5.6.--)\ U.\,M^1.\,M^2.------|--}{E^1.-E^3.\,OC\ (1.2.3.4.5.6.-)\quad U.\,M^1.\,M^2.------|--}$$

It contains 22 components of the 41 of the prototype. Because the components present in it are mostly more important than the absent ones the derivation of the wing-pattern of the genus from the prototype is doubtless. It is made evident by means of the diagram of the hypothetical Prototriphysa (fig. 306) constructed on the basis of the above formula.

The oligonome right end of the generic formula of *Triphysa* is of the same character as in the most other genera of palaearctic Satyridae as e.g. *Coenonympha* (p. 214) which differs from *Triphysa* only in its not being

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deprived of the first Discalia and Venosae. The fact should be emphasized that the last named genus is very small and does not show considerable variety in its patterns. Hence the above considerable degree of the realisation of the prototype in it is an evident proof of the intensity of prototypical tendencies within its limits, and consequently the genus should be regarded as rather prototypical.

CHAPTER XV.

MODIFICATIONS OF THE WING-PATTERN ON THE UNDERSIDE OF TRIPHYSA.

The modifications of the prototype on the underside of *Triphysa* wings are not numerous but some of them are of a very singular sort.

§ 1. EXTERNAE.

The disappearance of the second Externa has been indicated already in the preceding chapter. Also the first Externa has been mentioned which is either present (figs. 309, 310) or absent (fig. 325). The principal modification in the third Externa, i.e., its argentation has been also dealt with together with the broadening of the proximal half of the splitted E^3 and the supposed participation of the Umbra in the process (figs. 309, 322). Still another modification in the third Externa is the broadening of its silvery zone. In fig. 319 the stripe is more or less normally broad, while in fig. 320 it exhibits nearly double breadth. The brimming dark margins of E^3 show, however, no broadening at all remaining very narrow, and thus the process is evidently restricted to, the argentated parts of the component. In the same specimen the bent down shape of the cell-portions of the proximal half of E^3 deserves attention in the 4th, 5th and 6th cells.

§ 2. EYE-SPOTS.

We have now to pass on to the modifications in the eye-spots.

A. Dislocation on the forewing.

On the forewing of *Triphysa* the eye-spots undergoe a very singular dislocation. Fig. 309 shows the most prototypical position of the forewing eye-spots discovered in the genus. They all follow a direction parallel with the termen except those in the 6th and 1st cells which are somewhat dislocated. Now in fig. 317 the 3rd eye-spot is somewhat shifted basipetally compared to the

4th one. The same interrelation is seen in the next specimen (fig. 318), but besides this its 5th eye-spot has undergone basifugal dislocation so that the three anterior eye-spots follow a bent down line while the course of the total of the ocellar series reproduces an s-shaped figure more os less. The impression is born out that the 3rd and 5th eye-spots are displaced in opposite directions, and thus the ocellar series tends to be divided into two halves which are still kept together by means of the 4th eye-spot.

In the next specimen (fig. 319) the last named eye-spot plays the indicated rôle no more. It lies on the geometrical prolongation of the 5th and 6th eye-spots being the most distal of the three. On the contrary the 3rd eye-spot has become still more proximal than in the preceding specimen, and thus the distance between it and the 4th one is rather great. Thus the ocellar series has divided into two halves. The anterior half consists of three small eye-spots and is markedly oblique with regard to the termen. The posterior half formed by the two large eye-spots is also oblique to the termen but in a lesser degree that the anterior one, that is why the directions of the two halves form a considerable angle. The impression is born out that the ocellar series is influenced by two imaginary forces, one of them pressing basifugally on the 5th eye-spot, another pulling basipetally the 2nd one and thus both together causing the s-like twisting of the series (fig. 318). Then the break occurs at the point of the maximum tension, i.e., between the 3rd and 4th eye-spots (fig. 319). We can hardly suppose the above basifugal force to be directed against the 4th eye-spot as that being so the more distal position of the 5th eye-spot than that of the 4th one, as seen in fig. 318, would not be possible. We have besides to admit that like other pattern components the anterior half of the series of eye-spots is rectilinear and elastic in its nature. Having lost its rectilinear shape under the influence of the two forces the directions of which are opposite to one another it acquires again that shape after the break occurs and the basipetal force ceases to act upon it.

In the last specimen of our evolutionary series (fig. 320) the distance between the 3rd and 4th eye-spots has become still greater that being due both to the basipetal shifting of the 3rd eye-spot and basifugal dislocation of the anterior ones. The latter have come to lie near by the third Externa which, however, depends not only upon the dislocation of the eye-spots themselves but on the above described broadening of the silvery area of the stripe as well. The two halves of the series of eye-spots are so placed that without having seen their evolution one might suppose that they represent remnants of two parallel ocellar series, and thus the case reminds the dislocation in the eye-spots of *Coenonympha* (p. 220, figs. 245—252).

It is noteworthy that the series of the three anterior eye-spots which is rectilinear in fig. 319 has become curved again in fig. 320. This circum-

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stance may be explained as follows. Supposing the three eye-spots of fig. 319 to be approached to the third Externa the 4th eye-spot which is the nearest to the stripe should meet it sooner than the 3rd one which lies further from it. Now let us suppose the existence of a sort of repulsion between the eye-spots and third Externa which prevents these components from contact in the cases of their close approximation to each other. Some examples of such repulsion in various pairs of pattern components are recorded by KÜHN (1926) and by myself in my previous publications. That being so it is natural that the 4th eye-spot is stopped at some distance from E^3. If after this the 5th and 6th eye-spots be dislocated still more towards E^3 the result is that the series of three eye-spots looses its rectilinear form and becomes bent down again.

Thus we see that in *Triphysa* the series of eye-spots manifests the property of elasticity which has been observed by me in a number of examples in different components of other genera. It is worth of noticing that the described dislocation of the eye-spots of *Triphysa* is so to say reverse to the erebisation, in the latter process the 5th, or the 5th and 4th, eye-spots undergoing basipetal dislocation, while in *Triphysa* they move in an opposite direction as we have seen. If the erebisation, as we have seen in the foregoing chapters, is one of the very common modifications occurring in palaearctic Satyridae, that described in *Triphysa* is of a very singular sort and has not been met in any genus belonging to the indicated group.

On the other hand on comparing the dislocation of eye-spots in *Triphysa* forewing to that described in the hindwing of *Coenonympha* we notice a great resemblance between the two. The fact is that the ocellar series of *Coenonympha dorus* (fig. 250), if leaving its 6th eye-spot out of consideration, is divided into two parts which are so dislocated that the 4th eye-spot is shifted basifugally while the 3rd one basipetally. That state of the things is exactly the same we have just seen in *Triphysa*. Thus evidently the 4th vein serves a dividing line between the two parts of the ocellar series dislocating in the opposite directions. The modification in question does not occur in the genera of palaearctic Satyridae, and its occurrence in *Coenonympha* and *Triphysa* illustrates once more the close affinity between the two. But it is extremely interesting that the genera differ also from one another with regard to this modification as the division of the ocellar series along the 4th vein takes place on the hindwing in *Coenonympha* and on the forewing in *Triphysa* while in their respective other wings the series remains unaltered.

B. Combinations.

To complete the description of modifications in the eye-spots of *Triphysa* we have to mention only two specimens. In one of them (fig. 316) nothing

is left of the ocellar series on the forewing but the 2nd eye-spot. Though in the 6th cell a tiny vestige of the intra-Umbral circle is seen the latter does not contain, however, any remnant of eye-spot so that the ocellar formula of the specimen is: — 2. — — — — — — —. Exactly the same combination has been already described in *Coenonympha oedippus* (fig. 257) and in *Oeneis*.

Another noteworthy combination is that of a specimen of v. *nervosa* (fig. 324) whichs shows a "symmetrical" formula of eye-spots.

$$\frac{OC\ (— 2.\ 3. — — — — —)}{OC\ (— 2.\ 3. — — — — —)}$$

The presence of a few homologous eye-spots on both wings may be of great interest with regard to the ontogenetic development of the wing-pattern. Mostly the 2nd and 5th eye-spots take part in those combinations which is the case of *Triphysa* as well.

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§ 3. First Media.

In the first Media of *Triphysa* (M^1) two modifications should be considered. One of them is the marked concavity of the cell-portions of the stripe. In fig 307 many of them represent rectilinear bars while the remaining ones are but slightly bent in. In fig. 323 they are all regularly and markedly concave while in fig. 322 their curvations become still more pronounced and in some of the cells, as, e. g., in the 4th cell of the forewing, they acquire sagittate shape thus becoming elongated. The same concave shape of M^1 cell-portions we have already noticed in *Coenonympha oedippus* and *C. sunbecca* (figs. 285, 286, 299).

Another modification consists of the basifugal dislocation of the whole of the first Media. On both wings in fig. 321 M^1 is in a more or less prototypical position. In fig. 322 the stripe has markedly advanced in the basifugal direction. The modification is somewhat masked by the fact that in fig. 322 the M^1 portions are more curved and the eye-spots larger than in 321. But nevertheless it is quite evident that in the former the interspace between the eye-spots and M^1 is much narrower than in the latter while just the opposite is the case of the interspace between M^1 and the basal ends of all the cells crossed by it. The approximation of M^1 to the eye-spots is so close in fig. 322 that it somewhat resembles the condition when the latter are surrounded by the Umbra. Because however the Umbra surrounding the eye-spots is always exactly concentric with them (as, e.g., are the light rings in fig. 324), the indicated resemblance is but superficial.

§ 4. SECOND MEDIA.

The second Media undergoes on the hindwing of *Triphysa* a modification which has been described by me in *Satyrus* (1929 a, p. 600) under the name of triphysoid. In the latter genus the essence of the modification consists of a marked basipetal dislocation of the stripe along the subcostal nervure so that the protrusion thus formed tapers gradually towards its proximal end (text-fig. 11). In *Triphysa* itself the modification exhibits somewhat different and more complicated form. The most generalised status of M^2 discovered in *Triphysa* is that seen in fig. 315 where, however, the stripe is considerably modified already. The most important feature of M^2 in this specimen is that the stripe is divided into three parts, and the division depends not only on the existing veins but also on an atrophied one. The 7th cell-portion ($M^2 7$) begins from the basis of the 7th vein, runs anteriorly, then turns basipetally becoming parallel to the 8th vein and ends in the cell not far from the basis of the 7th cell.

In the discal cell there are two portions. One of them ($M^2 4a$) begins at the basis of the 7th vein, just opposite to the above mentioned beginning of $M^2 7$ and passes nearly along the subcostal vein closely approaching the latter by the proximal end. Another portion ($M^2 4p$) is more or less *U*-shaped the two branches of *U* being parallel to the subcostal vein.

Thus the second Media which in its prototypical form represents an uninterrupted stripe shows several interruptions in the hindwing of *Triphysa*. The fact, however, should be emphasized that the severed ends of the portions resulted from the interruptions behave differently, and from this point of view two parts may be discriminated in the component in question: one represented by $M^2 4p$, another consisting of $M^2 4a$ and $M^2 7$. The latter part should be regarded as a whole. Its subdivision into two by the light subcostal vein does not influence its direction at the point of its crossing over the vein that being readily seen from the fact that the hind end of $M^2 7$ and the fore end of $M^2 4a$ are both more or less perpendicular to the subcostal vein dividing them. If so it becomes evident that the common feature of the two described parts of M^2 is that all their ends (i.e., both ends of $M^2 4p$, hind end of $M^2 4a$ and fore end of $M^2 7$) have declined from their prototypical transverse direction and become more or less longitudinal. The described alterations in the hind end of $M^2 4p$ and fore end of $M^2 7$ are obviously dependent upon the median and 8th veins resp., i.e., the indicated cell-portions of M^2 are basipetally shifted along the indicated veins. This sort of modification does not represent anything exceptional. But more interesting are the fore end of $M^2 4p$ and hind (proximal) end of $M^2 4a$ both directed basipetally. It seems very likely that the shape of the indicated cell-portions depends upon a process similar to the just mentioned dislocation of the

stripes' ends along the nervures. There is only one important distinction as compared to usual cases: instead of an existing vein along which the dislocation takes place we see only a white line passing from the basal corner of the discal cell to the basis of the 5th cell between $M^2$4a and $M^2$4p and indicating the locus of an atrophied vein which corresponds to the media of Comstock's nomenclature while the median one of the present paper corresponds to Comstock's cubital vein. The atrophied vein, however, plays exactly the same rôle with regard to the cell-portions under consideration as the existing 8th vein does with regard to $M^2$7, i.e., the fore end of $M^2$4p and the hind end of $M^2$4a are dislocated along it basipetally while the remaining parts of them are more or less stationary. The circumstance seems unimportant that the discolated ends of the cell-portions do not adhere the atrophied vein as exactly the same interrelations exist, e.g., between the fore end of $M^2$7 and the 8th vein. The most interesting feature of the above status is that atrophied veins may influence the direction of stripes not less strongly than existing ones. This fact may be of importance in an investigation into the ontogenetic development of the wing-pattern and will be discussed in the chapter XVIII (p. 258).

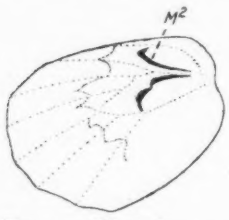

Fig. 10. Hindwing underside of *Satyrus huebneri* v. *dissoluta*. Basipetal elongation of the second Media (M^2) along the subcostal vein. (SCHWANWITSCH, 1929.)

It is obvious that the described modification of M^2 is not exactly corresponding with the triphysoid modification in *Satyrus* (text-fig. 10). Perhaps it is reasonable to mean by the triphysoid modification the basipetal dislocations of the portions of the second Media along the existing or vestigial veins.

It is very interesting that the same modification takes place on the forewing of *Triphysa*. M^2 in fig. 314 is partly parallel to the discal veins, partly to the median one, but the most important for us is that on the level of the 5th cell it emits a basipetal protrusion indicated with the right line of the two diverging from the letter. In fig. 312 it is still better pronounced and may be traced nearly up to the basis of the discal vein. Evidently this protrusion corresponds with the anterior branch of $M^2$4p in fig. 315 and the atrophied vein is marked with a stripe of light scales in both figs. 314 and 312. An accumulation of dark at the discal veins anterior to the said atrophied one most likely corresponds to $M^2$4a of the hindwing (fig. 315).

A further development of the modification takes place on the hindwing only. Supposing in fig 315 the $M^2$7 and $M^2$4a portions to be vanished and the two branches of the *U*-shaped $M^2$4p fused at their ends, the status seen in fig. 322 is resulted in where $M^2$4 represents an elongated oval. Closed

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rings often evolve from stripes but mostly they represent homomere complex components, i.e., arise from the coalescence of two neighbouring stripes in a given cell. A number of coalescences of this sort are described in my previous publications. But the case of *Triphysa* when the ring is built of a single cell-portion of a stripe owing to its extreme curvation is very singular of course. The only modification which is similar to this in a way is described by me in that of *Prepona* in which regular loops bud off from the third Externa and become independent ring-shaped components (1930 b, p. 323). But there are many differences not to be discussed here between the two modifications.

The described stage in the evolution of the second Media in *Triphysa* is the last in which the stripe still retains its strial character. The subsequent development leads to a total suppression of the latter, and is dependent on the coloration of the background. In fig. 315 the background of the interspace situated between the Mediae does not differ from that in other areas. In the hindwing in fig. 321 the indicated interspace is light in the almost whole of its extent while the area proximal to M^2 is dark. In fig. 324 almost the total of the wing becomes dark with the exception of light veinous stripes and two remnants of the interspaces between the Mediae, one lying in the 1st cell between $M^1$1 and $M^2$1, another in the discal and adjacent cells between M^1 and $M^2$4. In spite of the fact that both Mediae have lost their strial character and represent but boundaries of melanised areas they retain their typical positions. This is especially obvious in the discal cell as the long denticulated basipetal protrusion of the light area seen in fig. 324 undoubtedly corresponds with the similar protrusion in fig. 321 where the origin of the latter from M^2 is ready to see. A distorted remnant of the same protrusion is visible in the specimen represented in fig. 325 which exhibits the utmost degree of the melanisation of the underside discovered in *Triphysa,* and shows in its pattern only the indicated rudiment, light veinous stripes, two pairs of rudimentary eye-spots and a light terminal brim bordered by E^3. All the enumerated components except the veinous stripes are not much conspicuous, and generally the pattern may be described as longitudinal in which almost nothing is left of transverse components.

Finally it should be remarked that a tendency opposite to the above described one is noticeable in *Triphysa,* i.e., that of the darkening of the interspace between M^1 and M^2 and leaving light the rest of the background. Its best manifestation is seen in the hindwing in fig 322 which might serve a sort of negative to fig. 324.

CHAPTER XVI.

ON THE UPPERSIDE PATTERNS OF COENONYMPHA AND TRIPHYSA.

§ 1. UPPERSIDE OF COENONYMPHA.

The upperside of *Coenonympha* is not particularly interesting from the morphological point of view, at least at the present state of our knowledge of the wing-pattern. It is either totally melanised, or nearly so, or on the contrary quite light almost without pattern components (fig. 222), or if the latter are present neither their identification, nor connection with those of the underside represent any particular interest as, e.g., in *Coenonympha saadi* in which the interrelation between the upperside (fig. 213) and underside (fig. 212) is quite clear, and e.g. E^1, E^3, OC, U and M^1 are seen on both surfaces of the wings. In some *Coenonympha* forms the melanisation is restricted to certain wide areas the limits of which cannot be derived from any prototypical components as it is, e.g., in *Coenonympha leander* (fig. 223). The upperside of *Coenonympha iphis* (not figured) may be regarded typical of the genus. Its hindwing is melanised except the intra-Umbral rings and a narrow yellow strip parallel with and passing close by the termen. On the underside it is easy to discover the indicated strip owing to its coloration which is also yellow, and it is evident that it represents an interspace between E^3 and E^1.

Sometimes the pattern components and coloration of the underside are partly seen on the upperside owing to a partial transparency of the tender wings of *Coenonympha*. This is so, e.g., in *Coenonympha sunbecca*, the upperside of which (not figured) is nearly white, and the elegant pattern of the underside (fig. 299) is also seen above.

I have not met in *Coenonympha* anything similar to that complicated interdependence between the patterns of the upper and the under surfaces of the wing which render so interesting the respective analysis, e.g., in *Satyrus* or *Melanargia* dealt with in my previous publications. Therefore with regard to the *Coenonympha* upperside I restrict myself at present to a few remarks given in the above.

§ 2. UPPERSIDE OF TRIPHYSA.

The upperside of *Triphysa* are still less variable than those of *Coenonympha* as the genus is much smaller. They mostly represent a sort of reproduction of the corresponding undersides. The divergencies between the two are mostly

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not such as to be described here. We have to consider only the upperside of *Triphysa phryne* v. *dohrni* (fig. 326). Its relation to the respective underside (fig. 322) becomes quite clear, if comparing the two indicated figures. This is a typical example of a light upperside having dark underside, i.e., most of the pattern components seen in the former are those of the latter seen through the wing owing to its transparency as, e.g., the three anterior eye-spots on the hindwing, E^3, $M^2 4$, while only a few components exhibit independent pigmentation on the upperside as well, e.g., the eye-spots in the 2nd and 3rd forewing cells. Very interesting is the 4th forewing eye-spot which is seen in its main part through the wing but also possesses a small accumulation of dark scales at its distal margin. The described interrelations resemble those existing in *Coenonympha sunbecca*. On the other hand a sort of parallelism is noteworthy between the *Triphysa* upperside under consideration and that of *Coenonympha saadi* (figs. 212, 213) which consists of the 2nd and 3rd eye-spots on the forewing being enlarged and representing the most conspicuous components in the patterns of both forms while the remaining ones are not outstanding.

CHAPTER XVII.

OUDEMANS' PHENOMENON.

By the OUDEMANS' phenomenon peculiar interrelations are meant between the underside and upperside color-patterns (SCHWANWITSCH, 1931, p. 390). There are two forms of the phenomenon which result in two types of coloration named *Argynnis* and *Polygonia* forms according to the names of genera in which their manifestation is especially clear.

In *Argynnis* form two types of color-pattern may be recognized on the underside (text-fig. 11 C). One of them widely deviating from that of the upperside (text-fig. 11 D) occupies the apical part of the forewing (to the right from the arrows in 11 C) and the total area of the hindwing. Another is restricted to the rest of the forewing i.e. to its middle and basal area (to the left from the indicated arrows in 11 C). The last named type of color-pattern shows two remarkable pecularities: (1) it resembles very closely the color-pattern of the upperside, thus in this area the two surfaces of the wing being more intimately connected with each other than anywhere; (2) its area is concealed between the hindwings in a quietly sitting butterfly (text-fig. 11 E).

In *Polygonia* form the underside shows only one type of color-pattern (text-fig. 11 A) widely differing from that of the upperside (text-fig. 11 B), so that the degree of resemblance of the two surfaces of the wings is the

same everywhere. When quietly sitting the butterflies of *Polygonia* type expose nearly the total of the forewing underside (text-fig. 11 A).

The four genera dealt with in the present paper show a number of examples of the OUDEMANS' phenomenon. Let us consider the most interesting of them.

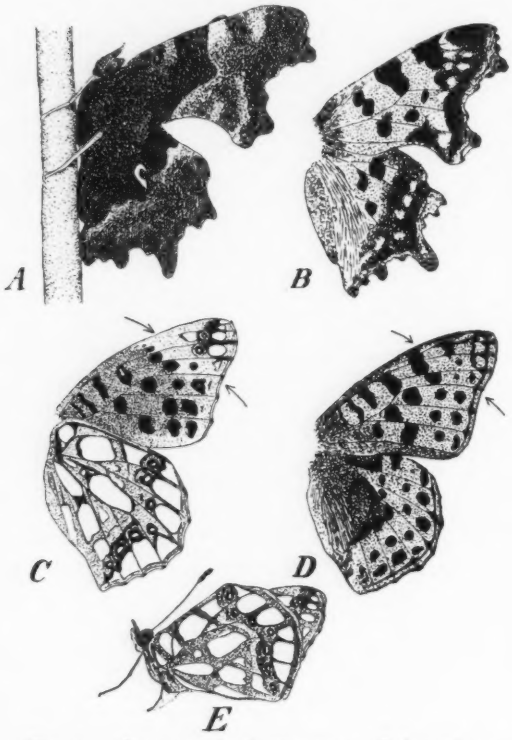

Fig. 11. OUDEMANS' phenomenon. *Polygonia c-album* shows one type of color-pattern on the underside (*A*) and another on the upperside (*B*). *Argynnis lathonia* shows two types of color-pattern on the underside (*C*), one on the hindwing and at the apex of the forewing (silvery markings), another on the remaining part of the forewing (black spots to the left from arrows); the latter type resembles greatly that of the upperside (*D*) and is concealed in a sitting butterfly (*E*). (SCHWANWITSCH, 1931.)

Pararge achine (fig. 2) with its very prototypical underside more resembles *Polygonia* type than that of *Argynnis*, the total of its underside showing in general the same color pattern. But the case of *achine* is not very typical, as the difference between the upperside (not represented in the plates) and underside is not great being mainly restricted to melanisation of the interspaces.

Pararge episcopalis (figs. 33, 34) is one of the best examples of *Argynnis* type. Two widely diverging color-patterns are readily seen on its underside (fig. 34). One of them in general grayish with numerous narrow stripes is restricted to the hindwing and the apical area of the forewing. Another is dark brown with a very few remnants of stripes. It is located in the middle and basal area of the forewing. The anterior end of the Umbra (*Up*) and the $E^3 + U$ component seem, however, also to belong here. The upperside of *episcopalis* (fig. 33) exhibits a closest resemblance to the underside in the last described area. The oblique white $U : M^1$ band crosses over the wing quite similarly in figs. 33 and 34 being only a little narrower in the former, and though the Medio-basal field is still darker on the upperside than on the under one, the general character of color-pattern is undoubtedly the same on both sides. On the contrary the two surfaces of the hindwing are widely differing in *episcopalis*. Below (fig. 34) a complicated polynome

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pattern is present, but no counterpart to it is seen on the almost totally melanised upperside (fig. 33) except for the narrow light interspace $E^2 : E^3$. Similar interrelations are observed in the apical part of the forewing where the only pattern components seen from above (fig. 33) are the 5th eye-spot and the white ocellar marking in the 6th cell. Thus it is evident that the resemblance between the two surfaces in *episcopalis* is very close in the middle and basal area of the forewing and quite not so in the rest. Or in other words a strong melanisation has suppressed the great majority of pattern components in the total of the upperside and to a great extent in the underside of the forewing. The exact correspondence of *episcopalis* to *Argynnis* type is out of doubt.

Pararge thibetana (fig. 35) belongs to the same category not being, however, so typical as the preceding species. Two characters are noteworthy in *thibetana* hindwing: the creamy almost white ground color and the fragmentation of stripes referred to (p. 161). They are more or less reproduced in the apical area of the forewing which is better to see in fig. 28. On the contrary the rest of the forewing exhibits yellow background and unfragmented stripes. Thus two color patterns exist in *thibetana* underside corresponding in their distribution to *Argynnis* type. The difference between them is, however, not very spectacular, the components being broad in both of them, while the upperside (not figured) adds almost nothing to the above data since its principal distinction from the underside is moderate melanisation of the majority of the interspaces not suppressing the pattern components totally. It should be noted, however, that on the forewing upperside a number of interspaces are as yellow as on the underside.

Pararge megera is one of the best examples of *Argynnis* type and has been briefly described by OUDEMANS himself (1903, p. 75). I can only confirm his data. On the underside (fig. 36) the hindwing and the apex of the forewing show narrow rather light stripes and grayish background. In the middle and basal part of the forewing the stripes are markedly heavier and darker while the background is yellow. The latter color-pattern is almost exactly reproduced on the upperside (fig. 37). The fact should be emphasized that the partial depigmentation of the eye-spots producing false Circuli (p. 152, *pOC*3 in fig. 12) occurs only in the hindwing and in the apical forewing eye-spots, while in the 5th forewing eye-spot which differs but slightly from its upperside counterpart (figs. 36, 37) the indicated process is either but slightly pronounced (fig. 11) or does not develop at all (fig. 10). Thus evidently the appearance of false Circuli is a part of the OUDEMANS' phenomenon.

Very similar status is observed in *Pararge egeria*. The middle and basal area of its forewing underside with its heavy stripes (fig. 47) resembles greatly the corresponding upperside (fig. 39), while the rest of the under-

side shows quite another color-pattern which in its dead leaf aspect differs much from the dark upperside.

Pararge eversmanni (figs. 52, 53) also falls under *Argynnis* type. The centro-basal area of the forewing underside is yellow, the stripes are degenerating, the posterior ends of M^1 and M^2 are lost, in the 5th and 2nd cells all the three Externae have fused together and in the 3rd one a peculiar $U3$ marking is present. All the described characters exist above as well (fig. 52) except for the fact that the degeneration of stripes has developed further and M^1, M^2, D^2, B have totally vanished. On the contrary the hindwing underside shows no trace of degeneration in its numerous pattern components and its background is white and grayish. It differs markedly from the yellow oligonome upperside of the hindwing. The apex of the forewing upperside exhibits the same state of the things as the hindwing.

Let us now pass to the next genus. In all *Epinephele* specimens represented in the plate III two color-patterns are readily seen on the underside. The total of the hindwing and the apex of the forewing show mostly dead leaf coloration and are typically striolated (figs. 91, 98, 100). Striolation may spread also along the forewing costa (fig. 96). Or the indicated areas are principally grayish with some white interspaces and show no striolation at all (figs. 94, 104) or nearly so (fig. 102). Another type of color-pattern is that of the middle and basic part of the forewing. Its salient features are ochreous yellow background and total absence of striolation. With regard to this all the *Epinephele* undersides represented in figs. 91—104 are quite alike. The described status corresponds exactly to the *Argynnis* form of the OUDEMANS' phenomenon. But the upperside of *Epinephele* does not show such typical bearing upon the underside as we have seen in *Pararge*. It is difficult to say, e.g., does the forewing of *pasiphaë* surpass the hind one with regard to the similarity of the upper and under surfaces, or the opposite is the case (figs. 93, 94). Rather a typical condition shows *janira* which has been described by OUDEMANS himself (1903, p. 75). The interspace between E^3 and M^1 is more melanised on the hindwing than on the forewing (fig. 97), and therefore the former is more differing from its underside than the latter. Also the degeneration of M^1 in the forewing underside of *tithonus* (fig. 100) and *davendra* (fig. 102) results most likely from the total disappearance of the component from the respective uppersides (figs. 99, 101). The above consideration shows that *Epinephele* affords very spectacular examples of the *Argynnis* form of OUDEMANS' phenomenon but the latter does not reach so high degree as in other genera.

The genus *Aphantopus* with its total or nearly so melanisation of the upperside (not figured in the plates) does not represent particular interest. Its uniform underside (figs. 106, 107) seems to belong to *Polygonia* type.

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In *Erebia* the OUDEMANS' phenomenon is better pronounced. Like *Epinephele* there is a number of cases when the striolation of the underside is mainly restricted to the hindwing and the apical part of the forewing, the rest of the latter being devoid of strioles. This is readily seen in figs. 113, 115, 155, 191, 195, 197, 199, 202. On the other hand the mutual relations of the above and below surfaces may be also very typical. In *Erebia cyclopius* underside (fig. 197) the forewing pattern consists only of a double eye-spot surrounded by the *iU* ring, the other components being suppressed by melanisation. The apex, however, is lightened and striolated. The upperside of the forewing (fig. 196) shows almost the same color-pattern, only *iU* is smaller. On the contrary the two surfaces of the hindwing are widely differing. Pronounced E^3, M^1 and M^2 are present below (fig. 197) while no trace of them is left on the totally melanised upperside (fig. 196). Quite the same is observed in the hindwing of *Erebia embla* (figs. 194, 195), while its forewing represents a sort of approximation to *cyclopius* condition, viz., E^3 and M^1 being totally lost above are still visible below. Thus obviously the resemblance of the two sides of *embla* forewing is much closer than that of its hindwing. The exact correspondence of the *iU* rings in figs. 194, 195 makes the indicated similarity particularly evident.

In *Erebia lappona* (figs. 190, 191) melanisation is still less advanced than in *embla*, so that the forewing Mediae are existing on both sides. But on the hindwing they are complete below and totally absent above thus again the difference between the two surfaces being closer in the forewing than in the hindwing. The lack of strioles and the darkish background in the great part of the forewing underside still enforce the described relations.

Very interesting is *Erebia ligea*. As we have seen in the description of its underside (p. 198) a pronounced *U* and two white interspaces $U:M^1$ and $M^2:Bm$ are present on the hindwing while on the forewing none of them is existing and only yellow $E^3:M^1$ is seen (fig. 193). Because the upperside of *ligea* (fig. 192) shows the same color-pattern as the forewing underside does, it is clear again that the hindwing underside differs widely both from its own upperside and from the two sides of the forewing, the three last named surfaces being all alike in accordance with the *Argynnis* form of OUDEMANS' phenomenon.

Erebia turanica (figs. 184, 185) though being very different from *ligea* in the general appearance and a number of other characters is, however, closely resembling the latter species with regard to the relation to the upper and under surfaces. Again there are white $U:M^1$ and $M^2:Bm$ interspaces which exist only on the hindwing underside, while the color-pattern of the three remaining surfaces is restricted to the yellow *iU* circles occupying the places of vanished eye-spots.

Finally *Erebia mani* also falls under *Argynnis* form of the OUDEMANS' phenomenon. Both sides of its forewing (figs. 202, 205) are very similar, and more or less the same type of color-pattern covers also the hindwing upperside. On the contrary the abundantly striolated underside of the hindwing devoid of contrasting colors belongs to another type of dead leaf character. Like many forms dealt with in the foregoing the striolation is also present near the costa and termen of the forewing.

The examples referred to of the OUDEMANS' phenomenon in *Erebia* are sufficiently typical. Some other forms of the genus as e.g. *pawlowskyi* (figs. 174, 188) show less pronounced interrelations but also seem to manifest the *Argynnis* form of the phenomenon. On the other hand *Erebia medusa* (figs. 200, 201) or *Erebia manto* v. *constans* (figs. 203, 204) with their far reaching identity of the upper and under surfaces can be hardly classified under any known form of the phenomenon. Such cases deserve a special investigation on a broad comparative basis. But at present they by no means diminish the value of the OUDEMANS' rule, as on the one hand we have got only the first formulations of it, and do not know whether it is general or not. On the other hand the already described examples of the rule are so numerous and interesting that a great importance of it is unquestionable.

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Passing now on the genus *Coenonympha* it should be pointed out that OUDEMANS himself (1903, p. 76) has described the *Argynnis* form of the phenomenon in *Coenonympha pamphilus* saying that "la couleur de la partie recouverte de l'aile-I est jaune ocré foncé, de même que la face dorsale. Les parties visibles sont grises". Thus *Coenonympha pamphilus* belongs to the *Argynnis* category.

Generally the manifestations of the OUDEMANS' phenomenon are not so striking in *Coenonympha* as in many other genera but nevertheless they are sufficiently typical. One of the best examples of the *Argynnis* form of the phenomenon represents *Coenonympha arcania* (fig. 290) in which the yellow coloration of the middle and basic areas of the forewing is contrasting to the generally brown hue of its own apex and of the total of the hindwing. The forewing shows neither numerous eye-spots nor light Umbro-Medial interspace ($U:M^1$) which are so characteristic of the hindwing. Thus there are two different types of color-pattern on *arcania* underside, and one of them restricted to the basic area of the forewing resembles closely its upperside (not figured). Similar status though not so pronounced is seen in *Coenonympha amaryllis* (fig. 279), in the three species represented in figs. 253—255 and in *Coenonympha myops* (figs. 218, 219). Interesting is *Coenonympha saadi* (figs. 212, 213) in which the OUDEMANS' phenomenon affects principally the eye-spots. Those of the underside (fig. 212) are generally pupillated. Those of the upperside (fig. 213) are black and depupillated. The latter condition occurs, however, in the 2nd and 3rd eye-spots of the forewing

underside which exhibit a much greater resemblance to their upper counterparts than all the remaining ones do. Thus again two types of eye-spots exist on the underside, those in the posterior cells of the forewing deviating from the rest just in the way required by the *Argynnis* form of the OUDEMANS' phenomenon.

There are also some not typical cases. E.g. in *Coenonympha semenovi* (figs. 295—297) there are again two types of color-pattern on the underside but the apex of the forewing neither differs markedly from the rest of the wing nor shows especial likeness to the hindwing, and thus the correspondence with the *Argynnis* form of the phenomenon is not exact.

Very interesting are the two forms of *Coenonympha sunbecca*. The typical form (fig. 299) may be undoubtedly classified under *Argynnis* category. The apical area of its forewing resembles closely the hindwing while the white tract extending over the three posterior cells of the forewing and entering the discal one differs markedly from the rest in the total absence of any components in it. On the other hand the white area reproduces exactly the condition existing on the upperside of *sunbecca*. But in the *alexandra* varietas of *Coenonympha sunbecca* (fig. 300) the described white area has greatly decreased, and is restricted to a very small area in the 1st cell and behind it. Almost the total of *alexandra* forewing does not differ in its color-pattern from the hindwing and the first Media, not extending posteriorly over the 3rd cell in fig. 299, is readily seen in the 2nd one in fig. 300. Consequently *alexandra* wing-pattern falls almost exactly under the *Polygonia* form of the OUDEMANS' phenomenon, and thus within the limits of a single species both forms of the latter occur. There are no data at my disposal as to the positions of rest of the bearers of the two above patterns. Were the OUDEMANS' rule be strictly followed by the behaviour of *sunbecca* forms those positions in *alexandra* and in forma typica should be different. But it is noteworthy that supposing the above occurrence of the two forms of the OUDEMANS' phenomenon to be reproduced, e.g., in *Argynnis* we should expect the silvery spots to be spread over the whole of its forewing underside. No such patterns are known among that abundant genus but perhaps they might be obtained by experiment.

Besides *Coenonympha sunbecca* v. *alexandra* there are some other even more typical examples of the *Polygonia* form of the OUDEMANS' phenomenon. The best of them is *Coenonympha hero* (fig. 291) with its eye-spots, white $U : M^1$ interspace and dark area proximal to M^1 which are quite alike on both wings. Also *Coenonympha oedippus* (fig. 289) belongs here though owing to the paucity of its pattern components it is less typical.

If both forms of the OUDEMANS' phenomenon occur in *Coenonympha* a glance at the figs. 321—325 in which *Triphysa* wings are represented suffices

to see that no *Argynnis* form of the phenomenon occurs in them, the type of the color-pattern being the same over the whole of their undersides.

Thus we have seen that the OUDEMANS' phenomenon is very frequent in the genera dealt with in the present paper. As to the degree of its development it seems reasonable to put the indicated genera in a definite sequence. *Pararge* affords the best examples of the *Argynnis* form of the phenomenon. *Erebia* follows it. The examples of *turanica* and *ligea* are very good of course. But some other *Erebia* forms as e.g. *embla* are less typical. Besides this the predomination of wide melanised areas makes many of the *Erebia* cases less spectacular than those of the other genera. In *Epinephele* very characteristic interrelations have been recorded on the underside, but it has been noted that their bearing upon the upperside patterns does not show sufficiently typical forms, and thus the genus should be regarded from this standpoint as comparatively backward. *Coenonympha* also exhibits numerous examples of the phenomenon but they are again somewhat less typical than those of *Pararge*. Finally the absence of typical OUDEMANS' relations in *Aphantopus* and *Triphysa* is not important owing to the paucity of color-patterns in these genera. The emphasis should be laid upon the fact that the great majority of cases dealt with in the foregoing are those of *Argynnis* form, and but a few examples of *Polygonia* form has been recorded: Thus the tendency to *Argynnis* form is decidedly preponderating in the genera in question and its manifestations are sufficiently numerous and characteristic.

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CHAPTER XVIII.

GENERAL DISCUSSION.

In the preceding chapters we have seen how the Nymphaloid prototype of wing-pattern is realised in the six genera of palaearctic Satyridae dealt with, and which are the ways of its evolution in them.

As to the realisation of the prototype some peculiar features of it are observed in almost all the genera dealt with in this and two preceding parts of my investigation on palaearctic Satyridae. The components of the prototype are always easily discernible as the modifications which they undergo are generally simple and mostly rather slight. It cannot be denied that a few of them are strong and result in wide deviations from prototypical status. But even those are never so complicated and difficult for analysis as, e.g., the processes observed in the highest South American Satyridae belonging to *Pierella* group (SCHWANWITSCH, 1928 a), or in *Catagramma* and *Prepona* groups of Nymphalidae (SCHWANWITSCH, 1930 a, 1930 b). Perhaps the most difficult case met in palaearctic Satyridae is the formation of false Circuli

in *Pararge* (p. 152) by the partial lightening of the eye-spots. But we have seen that even its analysis is comparatively simple. Thus with regard to the modifications of the prototype the palaearctic Satyridae cannot be numbered among the highest forms of the bulk of Nymphaloid butterflies.

Nevertheless they are highly specialized. I mean by this the number of components present. It is remarkable that some of the prototypical components are constantly absent in the majority of palaearctic Satyridae. The second Discalis and Basalis are the two stripes most liable to elimination in the group. They have been discovered only in *Pararge* while other genera show no traces of them. Somewhat more constant is the second Externa. It is present in several genera but in such a large genus as *Erebia* it is absent. On the other hand it has been shown already that in the genera having the second Externa it shows a very marked tendency to disappearance. Also the second Media though discovered in all the nine genera shows a very marked tendency to elimination. One could say, if summing up the above, that the absence of the second Externa and all the components proximal to the first Media is a typical feature of palaearctic Satyrids while the pronounced condition of the third Externa, first Media and a few eye-spots between them also belongs to the characters of the group. Meanwhile all the above mentioned components which tend to disappear in the latter do not belong to the rare ones and occur in the groups of *Pierella* and *Catagramma* which surpass greatly the palaearctic Satyridae with regard to the specialisation. Not being a general rule there are, however, some examples of strongest modifications occurring in the patterns of polynome formulae. This is e.g. the case of *Agrias sardanapalus* belonging to *Prepona* group in which the hindwing underside shows numerous modifications of most peculiar types but lacks only Granulatae and longitudinal stripes in its formula (SCHWANWITSCH, 1930, p. 371). The palaearctic Satyridae with their simple modifications and comparatively oligonome formulae seem to exemplify just as opposite direction of specialisation.

Another circumstance deserving a few remarks is the importance of the basifugal melanisation which has been repeatedly noted in the foregoing description. This phenomenon and the melanisation in general together with their connection with the Umbra and perhaps with some other prototypical components are all of great interest particularly for the upperside patterns. In dark colored genera like *Erebia* the rôle of melanisation is especially important. The cases of *Erebia cyclopius* or *Erebia embla* where nothing remains on the upperside but a few eye-spots and intra-Umbral circles are very typical of course of *Erebia* and some other genera too. But for the general knowledge of the nature of melanisation they are, however, less interesting than the cases like *Erebia herse* and *Erebia mani* where no dependence is established of the position of melanised areas upon the prototypical components.

Still more interesting is the case of the *Epinephele lycaon* upperside. We have seen in it (fig. 95) that the margin of basifugal melanisation passes obliquely across the border cells while the first Media is perpendicular to the dividing veins of the same cells and the crossing over of the two pattern components is resulted in, which resembles greatly most typical example of crossing over in *Pierella*. The first Media and the margin of the basifugal melanisation do not show in *Epinephele* any dependence upon each other regarding their direction. Therefore it seems not unlikely that the system of prototypical stripes and that of melanised areas are governed by quite different and independent systems of factors. This hypothesis would be in accordance with the view of SÜFFERT who thinks that besides transverse stripes some other pattern components do exist which are not exactly known and are particularly important in "painting large areas" (Flächenmalerei) (1929, p. 506). But I think that at present it is yet impossible to say whether the phenomena similar to basifugal melanisation are wholly independent from the prototypical components or not. Perhaps it is better to assume that some dependence exists but is so complicated that a special research is necessary to discover it. Such a research cannot be done, however, within the group of palaearctic Satyridae as the latter yields but a very few interesting cases, while the principal development of the phenomenon in question takes place in some exotic genera of Nymphaloid families which should be studied first to solve the problem. Until this work is done it seems hardly possible to give a more precise definition of the intra-Umbral rings than that already given in foregoing text. It should be remembered here that some vagueness of the indicated definition is due to the fact that at present in many cases no exact distinction can be drawn between the Umbra of the prototype and melanisation.

Melanisation is the most common way of darkening, but in *Pararge egeria* we have seen another way of the latter viz. the broadening of stripes or nigrism (figs. 38—41, 47). Owing to the participation of melanisation in *egeria* darkening the case is not pure, but nevertheless it is sufficiently typical.

As to the elimination, dislocation and other common rules of pattern evolution the examples of them in the foregoing description are so numerous and clear that no further comment is necessary. Some phenomena of this category deserve, however, special noticing as they were not described yet. One of them is the fragmentation of stripes recorded in the third Externa and first Media of *Pararge thibetana* (fig. 35). Being in its essence a form of division it differs from the ordinary form of the latter in the fact that no dislocation in the dissolving stripes is responsible for it, and it is defined in the foregoing as division *in loco* (p. 152) due to the disappearance of pigment from definite part of the stripes.

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Another modification is related to the just discussed one but owing to the components affected not being stripes it stands apart. I mean the formation of false Circuli in *Pararge megera* (figs. 10—12) which segregate from the eye-spots owing to the lightening of the subperipheric zones of the latter, the lightening being comparable to the above disappearance of pigment from the inter-fragmental zones of stripes.

The appearance of silvery coloration in the third Externa of *Coenonympha* and *Triphysa* also belongs to peculiar modifications of the prototype. The silvery coloration on the wings of Nymphaloid *Rhopalocera* is restricted to a few genera standing far from one another in the system, and the *Argynnis* case is the most known among them. As some of my unpublished data show, the silvery areas in *Argynnis* generally represent interspaces between the pattern components, while in *Coenonympha* and *Triphysa* we have adopted the view that the third Externa itself has become "silvergilt". The arguments favouring this hypothesis which are given in the chapter II need not be repeated here but it is evident that the *Coenonympha* and *Triphysa* condition interpreted in this way is very peculiar, though some analogies not to be discussed in the present paper might be possibly found among other genera.

A still another process restricted to the two last named genera to be pointed out here is the peculiar dislocation in the ocellar series of *Coenonympha* (figs. 245—252) and *Triphysa* (figs. 316—320). It is interesting from two points of view. We have seen that on the forewing of *Triphysa* it consists of the basifugal dislocation of the 4th and 5th eye-spots and the basipetal shifting of the 3rd one. Thus it represents, as we have pointed out, a reverse of the common ereboid dislocation. On the other hand this modification represents an example of the principle of combination, since in *Coenonympha* it takes place on the hindwing only the fore one showing more or less unaltered condition, while just the opposite is the case of *Triphysa* in which the dislocation is restricted to the forewing. This reminds the distribution of the pierellisation of Mediae in the *Pierella* group of South American Satyridae dealt with in one of my previous publications (1929 a). In the forewing of the genus *Pierella* both Mediae have undergone pierellisation but the hindwing of the same genus shows no inclination at all towards the said process, and its Mediae remain more or less unmodified. But in the genera *Caerois* and *Callitaera* belonging to the same group pierellisation takes place on the hindwings too (l.c. p. 515). Both in *Pierella* group and in *Coenonympha* and *Triphysa* a given modification may take place in a single wing leaving another inaffected and thus different combinations may be put in existence.

An example of the equifinal evolution also deserves to be noted here which consists of the disappearance of the first Media either in loco by

atrophy in *Coenonympha amaryllis* (figs. 275—283) or by dislocation and subsequent coalescense with the Circuli in *Coenonympha oedippus* (figs. 284—289). This state of the things resembles *Melanargia* in which the second Media can disappear either by depigmentation in loco or owing to basifugal dislocation and resultant fusion with the first Discalis (SCHWANWITSCH, 1931, p. 338).

Finally homomorphism also represents a peculiar phenomenon to be indicated here. We have seen that in *Pararge thibetana* (fig. 35) the eye-spots and fragments of different stripes look rather alike, or homomorphic, owing to their rather similar shapes and sizes and identical coloration. The modification is important regarding the habitus of butterflies. Besides the occurrence of homomorphism in some *Argynnis* forms like *lathonia* or *paphia* in which the fragments of different stripes look similar (KÜHN, 1926) it should be pointed out that the strong nigrism in some highest *Catagramma* patterns also results in their different components becoming similar to each other (SCHWANWITSCH, 1930 a, p. 235). *Pararge thibetana* can be hardly regarded as a nigristic form for it lacks the most typical features of nigrism viz. the intensely dark coloration of pattern components and the considerable decrease in the background area. The *thibetana* stripes and spots are brown of not a very dark shade and most of the interspaces between them are fairly wide. But undoubtedly highest *Catagramma* forms and *Pararge thibetana* have something in common which deserves a further elucidation, and it is noteworthy that in both genera the phenomena in question develop on the underside of hindwings.

As to the general properties of pattern components the six genera dealt with afford a great number of good illustrations. E.g. the elasticity of stripes manifests itself in its most typical forms in the strongly curved and characteristically attenuated cell-portions of E^3 in some *Pararge* and *Erebia* patterns (figs. 15, 124). Not less typical example of bending and stretching yield other *Pararge* forms in their second Media (M^2) which undergoes pierellisation and the resultant division into two parts (figs. 16—19) thus illustrating the common phenomenon of the rupture of distended stripes. We have seen that the ocellar series seems very flexible in *Coenonympha arcania* and the contact of the corresponding Circuli and third Externa on the whole extent of the series is resulted in (figs. 232—237) while in *Coenonympha hero* the same series appears more rigid and therefore the mentioned contact takes place at the ends of the series only, the latter being less curved than the Externa (figs. 238, 239). The elasticity of the ocellar series has been recorded in *Triphysa* too where the component in question first becomes bent, then a break occurs and the two resultant halves become quite independent from each other (figs. 317—320). Another example of the change of elastic properties of pattern components may be seen in the third

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Externa of some *Erebia* forms (text-fig. 5, p. 189). It is remarkable that a given stripe may be very flexible, strongly bent and therefore totally congruent with the wing in one species (text-fig. 5 C, p. 189), while in another (text-fig. 5 D) it looks rigid, shows almost no curvation corresponding to that of the wing-margin, and the loss of its portions thus located in extra-alar area is the result. But on the other hand we have seen that in some other forms of *Erebia* (figs. 148—151) the narrowing of the wing and the alterations in the Mediae are concomitant thus evidently a definite dependence being present between the wing shape and wing-pattern. If the independence of the wing-pattern from the wing manifests itself in *Erebia,* another most important property of pattern components, viz., their dependence upon each other is also recorded in the genera dealt with. We have seen the pressure of eye-spots upon the first Media in *Epinephele wagneri* (fig. 81) which is no less evident than the best examples of the phenomenon described in *Morpho* (SCHWANWITSCH, 1929b, p. 43). Another form of the same phenomenon is the flattening of the individual eye-spots and their Circuli due to their pressing against the third Externa seen in *Coenonympha dorus* (*C*5 in fig. 251). Both phenomena are not unparallelled as it has been pointed out already.

The fact just referred to bears also upon another category of phenomena, viz., that of the interaction of pattern components, in the present case the action of the third Externa upon the shape of the Circulus and eye-spot. As to the latter component it is not in an immediate contact with the Externa and the interaction of the two is put in existence through the medium of the interspace lying between them the latter thus being active in a way. The activity of the same interspace (*iU*) resulting in an extreme distension of the Circuli (*pC*) is also observed in *Coenonympha hero* (fig. 237). Different forms of the interaction of pattern components and of the activity of the interspaces are recorded in my previous publications and need not to be repeated here.

Still another general property of pattern components is their liberation in certain cases from the influence of the wing nervures. This is the case of the coalesced Circuli of *Coenonympha oedippus* and *amaryllis.*

In the generalised form of this coalescence the limits between the individual Circuli and the dividing nervures are congruent, while in the higher stages of the process (figs. 242, 244) the indicated limits are off the nervures, and thus the close dependence of the components in question upon the wing-venation does not exist more. A closest parallel to this is observed in the South American Nymphalid *Callicore* where the line of coalescence between one of the Circuli and a ringshaped component evolving from the first Media shows practically no bearing upon the nervures crossed by the

coalesced components and may occupy different positions on the wing irrespective of the nervures.

The fact of just an opposite character we have seen in *Triphysa* hindwing (fig. 315) where the basipetally directed ends of the second Media portions follow not only some of the existing nervures but also an atrophied one. This phenomenon is generally common and SÜFFERT illustrates it by a very good example of *Papilio diphilus* (1929, p. 315) in whose discal cell there are several longitudinal dark stripes passing along the "tracheal tubes". KÖHLER in his memoir referred to gives an excellent account of the development of venation in the larval wing rudiments of *Ephestia*. Now if a stripe, as, e.g., the second Media in *Triphysa,* shows an evident dependence upon the atrophied nervure the only possible conclusion is that the shape and position of the former are determined at a period when the latter is still existing, thus KÖHLER's data being corroborated about the early determination of pattern. If so the facts like the above pecularities in *Triphysa* and *Papilio diphilus* patterns may be of great service as to the identification of the period of localisation of the still invisible pattern components in the wing, and an investigation into the development of the wing-venation of properly chosen forms may considerably elucidate the mechanism of the color pattern. The above consideration shows how complicated the latter phenomenon is. We have seen that in one case the pattern becomes independent from the existing nervures while in another it exhibits on the contrary a dependence upon the disappeared ones.

Finally the most wonderful phenomenon of pattern evolution—that of positional inversion of components—also has been observed in palaearctic Satyridae. One example of it represents the passage of eye-spots through the third Externa in *Epinephele dysdora* (figs. 76, 77). Another fact seemingly belonging here as well is the crossing over of the first Media and basifugal melanisation in *Epinephele lycaon* (fig. 95).

Two observations should be noted here which are interesting from a more general point of view than the pattern mechanism. One of them is that two or more morphological processes may develop in opposite directions in a single series of specimens. We have seen that e.g. in *Erebia maurisius* v. *theano* (figs. 178—180) the narrowing of the Medial band, that is a deviation from the prototypical status, is accompanied by the disappearance of melanisation, that is by a restoration of prototypical status. Because the same phenomenon in a still clearer form has been recorded by me in *Satyrus* it seems reasonable to repeat the old truth that the interrelation between the evolution of single characters and that of whole organisms is very complicated.

Another observation concerns the uppersides of three *Erebia* forms namely *E. turanica* (fig. 185), *E. pawlowskyi* (fig. 188) and *E. maurisius* v. *theano* (fig. 189) in which we have seen that homologically different color-

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patterns greatly resemble one another (figs. 185, 188), while homologically similar ones exhibit quite different appearances (figs. 188, 189). This again shows how complicated may be the ways of the evolution of species.

To conclude the discussion we have to remember that the OUDEMANS' phenomenon especially in its *Argynnis* form is represented by excellent examples in our group but a particular attention should be paid to the fact that both this and *Polygonia* forms have been recorded within the limits of a single species namely that of *Coenonympha sunbecca* (figs. 299, 300).

In general the Nymphaloid prototype undoubtedly represents a basis of the great majority of the wing-patterns existing in the nine genera of the group of palaearctic Satyridae. The components of their patterns are on the one hand subject to the same modifications and reveal the same properties as those of other genera and families, on the other hand certain directions of their evolution are recorded only in these genera and thus impart to them their peculiar character.

It should be finally pointed out that the phenomena described in palaearctic Satyridae by the author afford a sufficient amount of facts to draw from it some conclusions on the evolution of wing-pattern which have no lesser bearing upon the evolutionary process in general than upon the special rules and interdependences discovered in the pattern. It is hoped, however, to deal with them elsewhere.

SUMMARY.

1. The wing-pattern of *Pararge, Epinephele, Aphantopus, Erebia, Coenonympha* and *Triphysa*—six Satyrid genera of *Lepidoptera Rhopalocera*—is dealt with in the present paper which represents a third part of the author's investigation (1929, 1931) upon nine palaearctic genera of Satyridae. The principal result of the work is that all the above genera derive the great proportion of their patterns from the Nymphaloid prototype constructed by the author (1924).

2. In the genus *Pararge* 36 pattern components are recorded out of 41 which the prototype is built of, thus the realisation of the latter in the genus being very complete. Particularly important is the presence of an eye-spot in the 8th cell of the forewing which component is the only absent in the pattern formula of the family of Satyridae given by the author (1924). Now that formula becomes absolutely complete like that of Nymphalidae.

3. A number of modifications of the components of prototype are observed in *Pararge*. The stripe named third Externa shows a typical convex bi-arcuate shape of its cell-portions, the same occurs in the second Externa. The latter may fuse with the first Externa. In the third Externa a particular phenomenon of fragmentation occurs consisting of the division of the stripe into

broad cell-portions without their dislocations. In the eye-spots the erebisation has been recorded, i.e. the basipetal dislocation of the 4th and 5th eye-spots of the forewing. The most interesting modification in *Pararge* eye-spots is the lightening of their sub-peripheric zones and the resultant division of each eye-spot into central and peripheric parts, the latter resembling the prototypical Circuli not being homologous to them. In the stripes named Mediae and Discalia several modifications are recorded met already in other genera like pierellisation, division of the second Discalis and some others. In *Pararge thibetana* the Medial band i.e. the first and second Mediae together undergoes fragmentation as a single component, which is the main cause of the peculiar habitus of the species.

Several types of upperside pattern evolve from the rather prototypical upperside of *Pararge megera*. The nigristic broadening of stripes, the melanisation of wide areas leaving light only a few interspaces and the elimination of a great majority of pattern components those are the main directions of the evolution leading to so different patterns as those of *Pararge egeria*, *P. maera* and *P. eversmanni*.

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4. In the genus *Epinephele* 25 components out of 41 have been discovered thus the realisation of the prototype in it being quite sufficient though less complete than in the preceding genus.

As to the modifications of the prototype in *Epinephele* the disappearance of the second Externa, the concave and convex forms of the third Externa cell-portions, the oblique position of the first Media on the forewing and some others are the principal occurring also in the other genera. Among the modifications apparently restricted to *Epinephele* the most interesting are the elongation of the 5th eye-spot the length of which almost trebles its breadth, and the peculiarly convex shape of the first Media on the hindwing of *Epinephele wagneri*. Especially interesting is the partial crossing of one of the eye-spots over the third Externa which process represents a beginning of the remarkable phenomenon of positional inversion of pattern components described by the author in *Prepona* (1930).

The upperside patterns of *Epinephele* belong principally to the Medio-External, Medio-Umbral and some other types which are common in palaearctic Satyridae. A case of crossing over of a prototypical stripe (first Media) and the margin of basifugal melanisation is recorded on the upperside of *Epinephele* which is ascribed to the apparently independent activity of two systems of pattern components.

5. In the genus *Aphantopus* 21 prototypical components have been discovered thus 20 being absent. Because the genus is very small and monotonous the above number should be considered as very high. The modifications in *Aphantopus* are not numerous, some of them remind the Eastern Satyrid *Lethe*.

6. The enormous genus *Erebia* shows 29 out of 41 components of the prototype thus the realisation of the latter in the genus being rather complete. But the absence of the second Externa in *Erebia* is noteworthy, which stripe is present in all the three above smaller genera.

Modifications of the prototypical components are numerous in *Erebia*. The third Externa exhibits different shapes of cell-portions, some of the latter may break off from the maternal stripe, the stripe may approximate very closely to the first Media and finally the cases of partial elimination of the third Externa should be regarded as incongruity of the wing and the wing-pattern. A peculiar budding is recorded in *Erebia* eye-spots which emit small protrusions breaking off from the maternal components. Similar budding occurs in the intra-Umbral circumocellar rings. When the eye-spots are absent the intra-Umbral circles may persist and evoluate as independent components. Erebisation of eye-spots is very typical of *Erebia* deriving from the latter its very name. The oblique position of the first Media and its fusion with the Umbra are noteworthy on the forewing while on the hindwing the Medial band may undergo either division or extreme broadening.

Melanisation of wide areas is one of the salient features of the genus and shows several forms. Both wings may undergo similar darkening. In the hindwing melanisation may be almost total, leaving, however, white a small area between the Umbra and first Media. In the forewing a case of parallel melanisation is recorded in four species. In *Erebia pawlowskyi* the interspaces between the third Externa and first Media dissolve into cell-portions and partly disappear while the rest undergoes melanisation; thus the proportion of the latter becoming high. On the contrary in *Erebia theano* the same interspaces and some others widen, thus the proportion of melanised areas becoming low. In the *Erebia turanica* the intra-Umbral circles devoid of eye-spots and the irregular fragments of the interspace between the Umbra and first Media are the only not melanised areas; a very peculiar pattern is resulted in.

8. In the uppersides of *Erebia* melanisation plays a principal rôle. It develops gradually leaving first intact the Medio-External interspaces, the latter darken in their turn so that only intra-Umbral circles remain, which finally disappear as well together with the eye-spots; such a total melanisation develops first on the hindwing. The relations between the upper and undersides of the same and of different wings may be very complicated as to the degrees of their melanisation.

By multiocellate uppersides those are meant in which numerous eye-spots or intra-Umbral circles are the most important components. In longitudinal uppersides the rôle of Venosae or at least of veinous fusions of transverse stripes is considerable; they may be also called inocellate because of the apparently typical lack of eye-spots in them. Wide light areas of *Erebia*

mani and related forms are independent from the prototypical components and depend upon the basifugal melanisation. The latter phenomenon cannot be investigated in palaearctic Satyridae as its principal development is restricted to some exotic groups.

9. The wing-patterns of *Coenonympha* and *Triphysa* have much in common. The numbers of prototypical components discovered in them are 25 and 22 resp.

10. Argentation of the third Externa of *Coenonympha* and *Triphysa* essentially consists of the change of the dark coloration of the stripe into a metallic silvery one. In *Coenonympha* the same stripe may fuse with the adjacent Circuli while the latter may fuse with each other and exhibit a sort of liberation from the prototypical dependence upon the wing nervures.

The series of eye-spots in *Coenonympha* and *Triphysa* divides into anterior and posterior portions which dislocate resp. basifugally and basipetally. The two genera mainly differ from each other in the fact that this division takes place on the hindwing in *Coenonympha* and on the forewing in *Triphysa*. This modification does not occur in other palaearctic Satyridae, while the common erebisation is recorded in *Coenonympha* as well. The combinations of eye-spots occuring in *Coenonympha* and *Triphysa* resemble in general those of allied genera.

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In the first Media several modifications are recorded. The coenonymphoid modification consists of the penetration of a small portion of the stripe into the discal cell of the hindwing. The tongue-like protrusion of the first Media in the anterior cells of the hindwing seems to occur in *Coenonympha* only. The common oblique position of the same stripe on the forewing is also recorded in *Coenonympha*. There are two ways of the disappearance of the first Media that either undergoes atrophy in loco or dislocates basifugally and fuses with the Circuli. In *Triphysa* the first Media may become convex in every cell, and dislocate as a whole basifugally. The second Media of *Triphysa* shows triphysoid modification, i.e., the ends of some of its cell-portions dislocate basipetally along the existing and atrophied veins. The latter circumstance is of interest since being influenced by atrophied vein the stripe evidently exists in the wing rudiment still before that atrophy takes place. One of the indicated cell-portions of the second Media can so bend that its ends coalesce and a ring is resulted in.

11. The analysis of several underside patterns is given which seem typical of the genus *Coenonympha*.

The presence of numerous eye-spots is the principal character of ocellate patterns occurring in several forms of the genus. The Umbro-Medial patterns are those in which the interspace between the first Media and the component termed Umbra is light. In *iphis* type of the underside the indicated interspace

disappears from all the cells but the 4th one on the hindwing where it represents an outstanding white marking.

The main feature of *semenovi* pattern is the course of the first Media which forms on the hindwing four broad protrusions fusing with the Umbra.

The principal characters of *sunbecca* pattern are the division of the Umbro-Medial interspace into cell-portions, the disappearance of the eye-spots combined with the preservation of the intra-Umbral circles in which the eye-spots normally lie and the white coloration of the background. A close homologous resemblance of this pattern to that of differently colored *Erebia turanica* is noteworthy.

The *mongolica* pattern evolves from the preceding one, and differs from it in the presence of eye-spots and disappearance of the great majority of the interspaces.

12. The OUDEMANS' phenomenon in the interrelation between the upperside and underside patterns formulated by the author (1931, cf. also text-fig. 11, p. 252) is illustrated by a number of examples in the genera dealt with.

13. The modifications recorded in the pattern components of the genera dealt with are mostly rather simple; the principal direction of specialisation in palaearctic Satyridae lies in the strong tendency of certain pattern components to disappear from the pattern.

14. The general properties of pattern components as elasticity, interaction, independence from the wing are illustrated by a number of examples. Even the positional inversion of components is recorded in *Epinephele*.

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EXPLANATION OF FIGURES.

All the figures except those specially indicated represent the undersides of specimens.

Key to lettering.

a — androconial area.
B — Basalis.
Bm — area of basifugal melanisation.
C — Circulus.
*C*3 — Circulus in the 3rd cell.
*C*4 — Circulus in the 4th cell.
C (4, 5) — Circuli in the 4th and 5th cells.
*C*5 — Circulus in the 5th cell.
*C*6 — Circulus in the 6th cell.
*cOC*3 — central part of the eye-spot in the 3rd cell.
*cOC*6 — central part of the eye-spot in the 6th cell.
D^1 — first Discalis.
D^2 — second Discalis.
$D^1 : M^2 4$ — interspace between first Discalis and second Media in the discal cell.
$D^2 : Bm4$ — interspace between second Discalis and basifugal melanisation in the discal cell.
dC — distal half of Circulus.
E^1 — first Externa.
E^2 — second Externa.
E^3 — third Externa.
$E^3 s$ — part of the third Externa separated from its maternal stripe.
$E^3 1$ — portion of the third Externa in the 1st cell.
$E^3 3$ — portion of the third Externa in the 3rd cell.
$E^3 4$ — portion of the third Externa in the 4th cell.
$E^3 6$ — portion of the third Externa in the 6th cell.
$E^3 7$ — portion of the third Externa in the 7th cell.
$E^1 + E^2$ — first and second Externae fused together.
$E^2 + U$ — third Externa and Umbra fused together.
$E^2 + U2$ — third Externa and Umbra fused together in the 2nd cell.
$E^1 : E^3$ — interspace between first and third Externae.
$E^2 : E^3$ — interspace between second and third Externae.
$E^2 : E^3 3$ — interspace between second and third Externae in the 3rd cell.

$E^3 : M^1$ — interspace between third Externa and first Media.

$E^3 : M^1 1$ — interspace between third Externa and first Media in the 1st cell.

$E^3 : M^1 2$ — interspace between third Externa and first Media in the 2nd cell.

$E : U$ — interspace between third Externa and Umbra.

G^1 — first Granulata.

G^2 — second Granulata.

iU — intra-Umbral circle.

$iU1$ — intra-Umbral circle in the 1st cell.

$iU6$ — intra-Umbral circle in the 6th cell.

$iU6 + (U : M^1 6)$—intra-Umbral circle fused with the Umbro-Medial interspace in the 6th cell.

J — Intervenosa.

M^1 — first Media.

M^{1*} — first Media of the underside seen through the wing from the upperside.

$M^1 1$ — first Media portion in the 1st cell.

$M^1 4$ — first Media portion in the 4th cell.

M^2 — second Media.

$M^2 1$ — portion of second Media in the 1st cell.

$M^2 4$ — portion of second Media in the discal cell.

$M^2 4a$ — anterior half of the second Media portion in the 4th cell.

$M^2 4p$ — posterior half of the second Media portion in the 4th cell.

$M^2 7$ — second Media portion in the 7th cell.

$M^1 + D^1$ — first Media and first Discalis fused together.

$M^1 + M^2$ — first and second Mediae fused together.

$M^1 + M^2 4$ — first and second Mediae fused in the 4th and discal cells.

$M^1 + M^2 (4.5)$ — first and second Mediae fused together in the 4th and 5th cells.

$M^1 + M^2 7$ — first and second Mediae fused together in the 7th cell.

$M^1 : M^2$ — interspace between first and second Mediae.

$M^1 : M^2 1$ — interspace between first and second Mediae in the 1st cell.

$M^1 : M^2 2$ — interspace between first and second Mediae in the 2nd cell.

$M^2 : Bm$ — interspace between second Media and basifugal melanisation.

$M^2 : Bm1$ — interspace between second Media and basifugal melanisation in the 1st cell.

$M^2 : Bm4$ — interspace between second Media and basifugal melanisation in the 4th cell.

$M^2 : Bm7$ — interspace between second Media and basifugal melanisation in the 7th cell.

$M^2 4 : D^2$ — interspace between second Media and second Discalis in the discal cell.

OC — eye-spot. Presence of eye-spots is designated by underlining the numbers of corresponding cells.

$OC(4.5)$ — eye-spots in the 4th and 5th cells.

$OC5$ — eye-spot in the 5th cell.

$OC6$ — eye-spot in the 6th cell.

pC — proximal half of Circulus.

$pOC3$ — peripheric part of the eye-spot in the 3rd cell.

$pOC6$ — peripheric part of the eye-spot in the 6th cell.

U — Umbra.

Ud — distal part of Umbra.

Up — proximal part of Umbra.

$U : M^1$ — interspace between Umbra and first Media.

$U : M^1 1$ — interspace between Umbra and first Media in the 1st cell.

$U : M^1 3$ — interspace between Umbra and first Media in the 3rd cell.

$U : M^1 4$ — interspace between Umbra and first Media in the 4th cell.

$U : M^1 6$ — interspace between Umbra and first Media in the 6th cell.

$U : M^1 1.2$ — interspace between Umbra and first Media in the 1st and 2nd cells.

$U : M^1 3.4$ — interspace between Umbra and first Media in the 3rd and 4th cells.

$U : M^1 7.8$ — interspace between Umbra and first Media in the 7th and 8th cells.

$U : U$ — interspace between two parts of Umbra.

V — Venosa.

Arabic ciphers designate numbers of border cells.

Arabic ciphers with dashes under them designate presence of an eye-spot in a given border cell.

PLATE I.

Parargе.

Fig. 1. Protoparargе: a hypothetical form illustrating the realisation of the Nymphaloid prototype in the genus *Parargе*. The formula of its pattern (generic formula) is given underneath—the forewing indexes are given above, the hindwing ones below the line, the missing components being replaced by dashes.

Figs. 2—10 show the existence of different components of the prototype (text-fig. 2, p. 147) in the representatives of *Parargе*.

Fig. 2. *Parargе achine* Scop. General prototypical habitus.

Fig. 3. *P. megera* v. *tigelius* Bon. 6th and 7th eye-spots are present on the forewing.

Fig. 4. *P. maera* L.
Fig. 5. *P. maera* L. } 8th eye-spot is present on the forewing.

Fig. 6. *P. eversmanni* Ev. Prototypical character of M^1, D^1, M^2, D^2, B.

Fig. 7. *P. megera* L. Prototypical M^1, M^2, D^1, D^2.

Fig. 8. *P. megera* v. *tigelius* Bon. Presence of G^1, G^2.

Fig. 9. *P. roxelana* Cr. Pronounced OC in the 7th cell.

B of the hindwing is present in fig. 32, V in fig. 39.

Figs. 10—12 formation of false Circuli. Fig. 10. *P. megera* L., fig. 11. *P. maera* v. *adrasta* Hb., fig. 12. *P. megera* v. *lyssa*. In fig. 10 $OC5$ is totally black, $OC6$ shows light coloration at the proximal border; in fig. 11 the total periphery of OC (4. 5) has become light, while $OC6$ has subdivided into $cOC6$ and $pOC6$ rings with a light zone between them; in fig. 12 $cOC6$, $pOC6$ are better pronounced while on the hindwing their homologues ($cOC3$, $pOC3$) are large, and $pOC3$ resembles $C3$ thus becoming a "false Circulus".

Figs. 13—15 ereboid dislocation in OC. Fig. 13. *P. achine* Scop., fig. 14. *P. hiera* F., fig. 15. *P. megera* L. In fig. 13 the OC series is regular, in fig. 14 the basipetal dislocation of the 5th and also of the 4th eye-spots is seen, which is more pronounced in fig 15.

Figs. 16—19 pierellisation of M^2. Figs. 16, 17. *P. hiera* F., figs. 18, 19. *P. maera* v. *menava* Moore. In fig. 16 the hind part of M^2 is basipetally dislocated; in fig. 17 it ($M^2 1$) lies on the level of D^2 but is yet connected with $M^2 4$; in fig. 18 $M^2 1$ and $M^2 4$ have separated from each other; in fig. 19 $M^2 1$ and D^2 nearly form a complex stripe.

Figs. 20—27 coenonymphoid form of M^3. Figs. 20—22. *P. eversmanni* Ev., figs. 23—27. *P. deidamia* Ev. M^1 is bent in fig. 20, the curvation is more pronounced in fig. 21 and still more so in fig. 22; the same modification develops more gradually in figs. 23—27.

Fig. 28. *P. thibetana* Obth. M^1 in the 3rd cell is markedly dislocated basifugally compared to its anterior portions (melanargoid modification).

Figs. 29, 30. *P. deidamia* Ev. M^1 shows rather prototypical direction in fig. 29 and oblique one in fig. 30.

Fig. 31. *P. praecusta* Leech. M^1 in the 1st cell has closely approximated to the termen, the beginning of which process is seen in fig. 28.

Fig. 32. *P. thibetana* Obth. Medial band (M^1, M^2) is widely interrupted in the 4th cell, D^2 is divided into two halves.

Fig. 33. Upperside
Fig. 34. Underside } of a specimen of *P. episcopalis* Obth.

In fig. 33 strong melanisation is seen, white $U : M^1$ represents the principal pattern component; in fig. 34 the direction of M^1 on the forewing is still more oblique than in fig. 30, the hind end of the stripe nearly reaches the termen.

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Fig. 35. *P. thibetana* Obth. E^1 and E^2 have formed $E^1 + E^2$ (their separate condition seen in figs. 31, 34), E^3 on the hindwing has dissolved into cell-fragments, the Medial band on the hindwing has dissolved into $M^1 + M^2$, $M^1 + M^2$ (4. 5) and posterior fragments (M^1, M^2); the eye-spots and the fragments of E^3, $M^1 + M^2$ and D^2 look similar (homomorphism).

Fig. 36. Underside } of a specimen of *Pararge megera* L.
Fig. 37. Upperside }

Fig. 36 differs from the prototype only in a few characters as e.g. convex bi-arcute E^2 and E^3 cell-portions, false Circuli in eye-spots, oblique M^1 on the forewing and absence of some components. Fig. 37 differs from its underside in the general broadening of stripes, absence of false Circuli, absence of hindwing M^2, D^2 and a few other characters.

Figs. 38—40 uppersides of *P. egeria* L. The underside corresponding to fig. 39 is represented in fig. 47.

There is considerable difference between figs. 37 and 38 in the habitus, but their homologous relations are close. The main distinctions of fig. 38 from fig. 37 are: in the forewing the basifugal protrusion of M^1 along the 4th vein, the presence of $E^3 + U$ and Bm; in the hindwing the shortening of $U : M^1$ owing to the fusion of basal melanised area with U in posterior cells.

The principal distinctions of fig. 39 from fig. 38 are the general broadening of stripes and the division of uninterrupted interspaces into cell-fragments.

In fig. 40 all the interspaces proximal to M^1 have disappeared (viz. $D^1 : M^2 4$, $M^1 : M^2 2$, $M^1 : M^2 1$) except narrowed $M^2 4 : D^2$, those distal to M^1 are well individualised and decreased in size compared with fig. 39.

PLATE II.

Pararge and Epinephele.

Fig. 41. Upperside of a male specimen of *Pararge egeria* v. *xiphioides* Stgr. Some interspaces absent in fig. 40 are present in fig. 41 ($D^1 : M^2 4$, $M^1 : M^2 2$, $M^1 : M^2 1$, $M^2 : Bm 1$) and *v. versa* ($E^2 : E^2 3$).

Figs. 42—46. Melanisation on the upperside. Fig. 42. *P. megera* L., fig. 43. *P. maera* v. *sicula* Stgr., fig. 44. *P. maera* v. *adrastoides* Bien., fig. 45. *P. maera* L., fig. 46. *P. maera* L.

Fig. 42 differs from fig. 37 in a stronger melanisation chiefly in the hindwing; in fig. 43 owing to a further melanisation M^1 has disappeared from the hindwing, on the forewing the area proximal to M^1 is quite dark, iU has formed on the hindwing owing to the addition of Umbral elements to E^3; in fig. 44 melanisation has resulted in the disappearance of D^1, M^2, D^2 from the forewing and of E^1, E^2 from both wings; in fig. 45 general melanisation is slighter so that D^1, M^2 on the forewing and M^1 on the hindwing are still visible, but the area between E^3 and M^1, light in fig. 44, is darkened in fig. 45; in fig. 46 strong melanisation suppresses everything but OC and iU.

Fig. 48. *P. dumetorum* v. *fulvescens* Alph. Upperside. Partly resembles *egeria* but differs from it in the almost uninterrupted $U : M^1$ and absence of $M^1 : M^2$.

Figs. 49, 50. *P. deidamia* Ev. In fig. 49 light $U : M^1$ on the forewing and its absence on the hindwing; in fig. 50 darkened $U : M^1$ in both wings.

Fig. 51. *P. maera* v. *menava* Moore. Upperside. Atrophy of E^3, E^2 and U on the forewing.

Fig. 52. Upperside
Fig. 53. Underside } of a specimen of *P. eversmanni* Ev.
Elimination of a greater part of components from the upperside.

Figs. 54—56. *Pararge clymene* v. *roxandra* H.S. Numerous components are present in fig. 54, they become faint in fig. 55, most of them disappear in fig. 56 but $U : M^1 4$ remains in spite of the absence of typical U and M^1.

Fig. 57. Protepinephele. Explanation as in fig. 1.

Figs. 58—68 show the existence of different components of the prototype in the representatives of *Epinephele*.

Fig. 58. *Epinephele amardea* Ld. General prototypical habitus.
Fig. 59. *E. pasiphaë* Esp. Numerous *OC* and typical *U*.
Fig. 60. *E. cadusia* Ld. Rectilinear E^3.
Fig. 61. *E. rueckbeili* Stgr. Upperside. None fused *OC* in the 4th and 5th cells.
Fig. 62. *E. pasiphaë* Esp. Presence of D^1.
Fig. 63. *E. hilaris* Stgr. M^2 in the 1st cell.
Fig. 64. *E. naubidensis* Ersch, Rather a prototypical E^3.
Fig. 65. *E. rueckbeili* Stgr. *OC* in the 6th cell.
Fig. 66. *E. lycaon* v. *intermedia* Stgr. *OC* in the 2nd cell.
Fig. 67. *E. rueckbeili* Stgr. *OC* in the 4th cell.
Fig. 68. *E. sp.* Presence of D^1.
Fig. 69. *E. pasiphaë* Esp. Diffused E^2.
Fig. 70. *E. pulchella* v. *pulchra* Feld. Convex E^3 cell-portions.
Fig. 71. *E. narica* v. *conjungens* Alph. Concave bi-arcuate E^3 cell-portions.

Figs. 72, 73. Ereboid dislocation of *OC*. Fig. 72. *E. tithonus* L.—*OC* in a rather prototypical position. Fig. 73. *E. pasiphaë* Esp.—*OC* in the 4th and 5th cells dislocated basipetally.

Fig. 74. *E. hilaris* Stgr. Convex E^3 cell-portions.
Fig. 75. *E. narica* v. *conjungens* Alph. Concave bi-arcuate E^3.

Figs. 76, 77. Positional inversion in *E. dysdora* Ld. Fig. 76. Prototypical position of $OC1$, fig. 77. $OC1$ has crossed over $E^3 + U$ and entered $E^1 : E^3$ (inverted positions of E^3 and *OC*).

Figs. 78—82. Elongation of $OC5$ on the upperside. Fig. 78. *E davendra* Moore, fig. 79 *E. wagneri* v. *mandane* Koll., fig. 80. *E. wagneri* H.S., fig. 81. *E. wagneri* H.S., fig. 82. underside of a specimen of *E. wagneri* H.S. $OC5$ is normal in fig. 78, elongated in fig. 79, still more so in fig. 80 and very long in fig. 81. It is unmodified in fig. 82. When elongating $OC5$ presses upon M^1 (fig. 81).

Figs. 83—86. Oblique position and yellow coloration of M^1. Fig. 83. *E. davendra* Moore, figs. 84, 85. *E. wagneri* H.S., fig. 86. *E. janiroides* H.S. Prototypical course of M^1 in fig. 83 becomes more and more oblique in figs. 84—86. M^1 is dark brown in fig. 85, its middle is yellow in fig. 86.

PLATE III.

Epinephele, Aphantopus, Erebia.

Figs. 87—90. Bending down of M^1. Figs. 87, 88. *Epinephele dysdora* Ld., fig. 89. *E. wagneri* v. *mandane* Koll., fig. 90. *E. wagneri* H.S. The gradual curvation of M^1 is evident in the series.

Figs. 91, 92. *Epinephele lycaon* v. *intermedia* Stgr. M^1 is present in fig. 91 and absent in fig. 92.

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Fig. 93. Upperside
Fig. 94. Underside } of a specimen of *E. pasiphaë* Esp.

Light $E^3 : M^1$ between two dark areas, one distal to E^3 another proximal to M^1, on the upperside.

Fig. 95. Upperside
Fig. 96. Underside } of a specimen of *E. lycaon* v. *intermedia* Stgr.

In fig. 96 darkening of $E^3 : M^1$ on the hindwing, a dark streak crosses it along the 4th vein on the forewing, *Bm* crosses over M^1.

Fig. 97. Upperside
Fig. 98. Underside } of a specimen of *E. janira* L.

In fig. 97 $U : M^1$ on the hindwing and apparently the same on the forewing.

Fig. 99. Upperside
Fig. 100. Underside } of a specimen of *E. tithonus* L.

The pattern in fig. 99 principally consists of a double *OC* and dark brim bordered by E^3.

Fig. 101. Upperside
Fig. 102. Underside } of a specimen of *E. davendra* Moore.

In fig. 101 the forewing resembles that of fig. 99, the hindwing is considerably melanised though E^1, E^3, U, M^1 are still visible.

Fig. 103. Upperside
Fig. 104. Underside } of a specimen of *E. wagneri* H.S.

In fig. 103 the elongated *OC* in the forewing is the only conspicious pattern component, the rest being nearly totally melanised.

Fig. 105. Protaphantopus. Explanation as in fig. 1.

Fig. 106. *Aphantopus arvensis* Obth. General prototypical habitus.

Fig. 107. *A. hyperanthus* v. *bieti* Obth. Suppression of all the stripes by melanisation.

Fig. 108. *A. hyperanthus* L. Double *OC* in the 2nd cell, basipetal dislocation of *OC* in the 5th one, presence of *OC* in the 6th cell.

Fig. 109. *A. hyperanthus* L. Presence of *OC* in the 4th cell.

Fig. 110. *A. hyperanthus* L. Prototypical E^2.

Fig. 111. *A. hyperanthus* L. Prototypical E^2, presence of M^2, interruption of M^1 by the discal cell.

About some other modifications in *Aphantopus* see text p. 182.

Fig. 112. Proterebia. Explanation as in fig. 1.

Figs. 113—121 show the existence of different components of the prototype in the representatives of *Erebia*.

Fig. 113. *Erebia fasciata* v. *semo* Gr. Gr. Strong E^3, prototypical M^1, M^2.

Fig. 114. *E. afra* Esp. Numerous *OC*.

Fig. 115. *E. lappona* Esp. General prototypical habitus.

Fig. 116. *E parmenio* Boeb. Rather a prototypical E^3.

Fig. 117. *E. lappona* Esp. Presence of D^1.

Fig. 118. *E. medusa* v. *transiens* Stgr. Undislocated *OC* series.

Fig. 119. *E. parmenio* Boeb. Prototypical E^3.

Fig. 120. *E. manto* Esp. Presence of D^1.

Fig. 121. *E. afra* Esp. Prototypical *OC* series.

Figs. 122—124. Basipetal dislocation of E^3 in *E. ocnus* Ev.

E^3 is in prototypical position in fig. 122, approximated to M^1 in fig. 123, still more so in fig. 124.

Figs. 125, 126. *E. embla* Thnbg. Budding of E^3. In fig. 125 E^3 forms basipetal protrusion in the 4th cell; in fig. 126 it (E^3s) has separated from E^3.

Figs. 127, 128. *E. cyclopius* Ev. Fusion of E^3 and M^1. E^3 cell-portions are bent in in fig. 127, one of them has fused with M^1 in fig. 128.

PLATE IV.

Erebia.

Figs. 129—132. Budding of *OC*. Figs. 129, 130. *Erebia embla* Thnbg., fig. 131. *E. afra* Esp., fig. 132. *E. turanica* v. *laeta* Stgr.

In fig. 129 the 4th and 5th *OC* form basifugal protrusions, in fig. 130 the latter have elongated, in fig. 131 the small marking distal to the 5th evidently originates from the corresponding protrusion; in fig. 132 similar budding is seen in *iU* in the 4th, 5th and 6th cells.

Figs. 133—138. Erebisation of *OC* in *E. embla* Thnbg. The gradual basipetal dislocation of the 4th and 5th *OC* is readily seen in the figures, fig. 138 shows very proximal position and the direction parallel to the posterior *OC*.

Figs. 139—142. Erebisation of *OC* in *E. afra* Esp. The development of the basipetal dislocation of the 4th and 5th *OC* is readily seen in the figures, in fig. 142 they lie far from the rest of *OC* and form an angle to it.

Fig. 143. *E. gorge* Esp. Medial band (M^1, M^2) is interrupted in the 1st cell.

Figs. 144—147. Broadening of the Medial band (M^1, M^2) in *E. parmenio* Boeb. The interspace between M^1 and M^2 is narrow in fig. 144, somewhat broader in fig. 145, still broader in fig. 146 and very broad in fig. 147.

Figs. 148—151. Broadening of Medial band (M^1, M^2) in *E. ocnus* v. *mongolica* Ersch. (figs. 148, 149) and *E. sibo* Alph. (figs 150, 151). In fig. 148 M^1, M^2 is of prototypical shape; in fig. 149 it is bent; in fig. 150 more bent, broadened in the middle and narrowed in the 1st cell; in fig. 151 the indicated characters are still more pronounced.

Figs. 152, 153. *E. neoridas* Bsd. M^1 is roughly parallel to the termen in fig. 152 and forms an angle to it in fig. 153.

Fig. 154. *E. cyclopius*. Fusion of *U* with M^1.

Figs. 155—157. Melanisation in both wings. Fig. 155. *Erebia pronoë* Esp. 156, 157. *E. sedakovii* Ev. In fig. 155 ground color is light, in fig. 156 melanisation is pronounced in the areas distal to E^3 and proximal to M^1, in fig. 157 $E^3 : M^1$ is the only light area on the forewing, the rest is strongly melanised, all the stripes, however, remain visible.

Figs. 158—165. Two ways of melanisation in hindwings. Fig. 158. *E. ligea* v. *ajanensis* Mén., figs. 159, 160. *E. ligea* L., figs. 161—163. *E. edda* Mén. $U : M^1$, broad in fig. 158, narrows in fig. 159 and represents two narrow vestiges in fig. 160, which is accompanied by a strong darkening of the total of the wing. In figs. 161—163 gradual general melanisation is observed except for the oval $U : M^1 4$.

Figs. 164—171. Parallel melanisation of the forewing in four species. Figs. 164, 165. *E. embla* Thnbg., figs. 166, 167. *E. edda* Mén., figs. 168, 169. *E. parmenio* Boeb., figs. 170, 171. *E cyclopius* Ev. E^3 and M^1 are visible in figs. 164, 166, 170 and suppressed by melanisation in figs. 165, 167, 171; the same is the case of M^1 in figs. 168, 169 resp. (About the loss of the hind end of E^3 in fig. 170 cf. text-fig. 5, p. 189.)

Figs. 172—177. *E. pawlowskyi* Mén. $E^3 : M^1$ is fairly broad in fig. 172 and in the hindwing in fig. 173; in fig. 174 the total of $E^3 : M^1$ is divided into cell-fragments, the latter have decreased in fig. 175, still more so in fig. 176, while in fig. 177 three ve-

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stigial $E^3 : M^1$ represent the only remnants of light background, all the rest being totally melanised.

Figs. 178—180. *E. maurisius* v. *theano* Tausch. Medial band (M^1, M^2) is of normal breadth in fig. 178, narrowed in fig. 179 and very narrow in fig. 180 thus the proportion of light background becoming high.

PLATE V.

Erebia and Coenonympha.

Figs. 181—183. *E. turanica* v. *laeta* Stgr. In fig. 181, *OC* are pronounced, $U : M^1$ uninterrupted; in fig. 182 *OC* are vestigial, $U : M^1$ dissolved into fragments; in fig. 183 *OC* are nearly absent, $U : M^1$ fragments decreased and irregularly shaped, $M^2 : Bm$ disappeared.

Fig. 184. *Erebia turanica* v. *tristis* Gr. Gr. Further atrophy of *OC* and $U : M^1$ begun in figs. 181-183.

Figs. 185—187. Multi-ocellate uppersides.

Fig. 185. Upperside of *E. turanica* v. *laeta* Stgr. Multi-ocellate pattern without *OC*, the shape and position of *iU* being closely dependent upon the absent *OC*. Fig. 186. Upperside of *E. turanica* v. *jucunda* Püng. differs from the preceding figure in its expanded *iU* on the forewing. Fig. 187. Upperside af *E. afra* Esp. Numerous *OC* are the principal part of the pattern.

Figs. 188, 189. Inocellate uppersides showing no *OC*. Fig. 188. *E. pawlowskyi* Mén. $E^3 : M^1$ fragments are small, the rest being totally melanised. Fig. 189. *E. maurisius* v. *theano* Tausch. $E^3 : M^1$ is very broad, another light area is proximal to M^2.

Fig. 190. Upperside
Fig. 191. Underside } of a specimen of *E. lappona* Esp.

In fig. 190 the forewing is prototypical showing numerous components differing but slightly from fig. 191, the hindwing in fig. 190 is strongly melanised.

Fig. 192. Upperside
Fig. 193. Underside } of a specimen of *E. ligea* v. *ajanensis* Mén.

In fig. 192 $E^3 : M^1$ is the only light interspace, in fig. 193 this is so only on the forewing while on the hindwing owing to the existence of *U* there is no $E^3 : M^1$ but there are $U : M^1$ and $M^2 : Bm$.

Fig. 194. Upperside
Fig. 195. Underside } of a specimen of *E. embla* Thnbg.

Four *OC* and *iU* are the only pattern components in fig. 194, while numerous components are present in fig. 195.

Fig. 196. Upperside
Fig. 197. Underside } of a specimen of *E. cyclopius* Ev.

Only two coalesced *OC* and *iU* are present in fig. 196 while some other components are existing in fig. 197 which are, however, less numerous than in fig. 195.

Fig. 198. Upperside
Fig. 199. Underside } of a specimen of *E. hades* Stgr.

Only one pupillated *OC* is existing in fig 198, the rest being totally melanised, fig. 199 shows more pattern components.

Fig. 200. Upperside
Fig. 201. Underside } of a specimen of *E. medusa* F.

Multi-ocellate pattern (cf. figs. 185—187). Several *OC, iU* and other components are existing in fig. 200. Its resemblance to fig. 201 is remarkable.

Fig. 202. *Erebia mani* Nicev. var. (The upperside of the same specimen is represented in fig. 205.)

Fig. 203. Upperside
Fig. 204. Underside } of a specimen of *E. manto* v. *constans* Elw.

Total melanisation of both sides in both wings.

Fig. 205. *E. mani* Nicev. var. Upperside (the underside of the same specimen is represented in fig. 202). *Bm* borders proximally the light peripheric area on the hindwing.

Figs. 206—210. Development of light area on the forewing. Fig. 206. *E. mani* Nicev. Upperside (the underside of the same specimen is represented in fig. 209).

Fig. 207. *E. hersc* Gr. Gr. Upperside.

Fig. 208. *E. mani* v. *fasciata* Stew. Upperside (the underside of the same specimen is represented in fig. 210).

Fig. 209. *E. mani* Nicev. (the upperside of the same specimen is represented in fig. 206).

Fig. 210. *E. mani* v. *fasciata* Stew. (the upperside of the same specimen is represented in fig. 208).

In fig. 210 M^1 is typical, in fig. 209 the anterior part of the dark area bordered by M^1 has become lighter than the rest, in fig. 206 the mentioned part has disappeared and generally no undoubted M^1 is seen, in fig. 207 the light area proximal to E^3 has crossed over the line of the disappeared M^1 and reached the basis of the wing being thus bordered by *Bm*. In fig. 208 melanisation of the light area is seen.

Fig. 211. Protocoenonympha. Explanation as in fig. 1.

Fig. 212. *Coenonympha saadi* Koll. General prototypical habitus.

Fig. 213. Upperside of the specimen represented in fig. 212.

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PLATE VI.

Coenonympha.

Figs. 214—223 show the existence of the components of the prototype in the representatives of *Coenonympha*.

Fig. 214. *Coenonympha amaryllis* Cr. Numerous eye-spots.

Fig. 215. *C. sunbecca* Ev. *iU* in 7th cell.

Fig. 216. *C. oedippus* F. Eye-spot in 1st cell.

Fig. 217. *C. hero* L. Eye-spot in 1st cell.

Figs. 218, 219. *C. myops* v. *tekkensis* Stgr. Presence of M^2 and D^1.

Figs. 220, 221. *C. corinna* Hb. Pronounced M^2.

Fig. 222. *C. leander* Esp. Presence of D^1.

Fig. 223. *C. leander* Esp. (upperside). Presence of *V*.

Figs. 224, 225. Argentation (appearance of silvery coloration) of E^3 in *Coenonympha thyrsis* Frr. In fig. 224 E^3 is totally dark, in fig. 225 silvery coloration has appeared in all E^3 cell-portions but that in the 1st forewing cell.

Figs. 226—228. Argentation of E^3 in *C. amaryllis* Cr. In fig. 226 E^3 is totally dark on the forewing but a silvery brim accompanies it on the hindwing; in fig. 227 the brim has broadened on hindwing and made its appearance on forewing; in fig. 228 silvery brim is broad on both wings.

Figs. 229—231. Argentation of E^3 in *C. oedippus* F. In fig. 229 E^3 contains silvery scales in its middle in all the cells but the 1st on forewing; in fig. 230 the argentated middle area of E^3 has widened; in fig. 231 it is very wide.

Figs. 232—237. Fusion of E^3 and dC in *C. hero* L. (figs. 232—235) and *C. hero* v. *perseis* Ld. (figs. 236, 237). dC is far from E^3 in fig. 232, has approached to it in fig. 233, the two are in contact in fig. 234 and fused together in fig. 235; about the absence of pC in fig. 236 see text p. 217; in fig. 237 iU interspaces are much expanded.

Figs. 238, 239. Non flexible ocellar series in *C. arcania* L. In fig. 238 C and E^3 show no contact, in fig. 239 C and E^3 are in contact in the 1st and 4th cells, but show no contact in the 2nd and 3rd ones thus the ocellar series not being bent in spite of its approximation to E^3. Meanwhile in figs. 232—235 owing to a greater flexibility of the series the contacts exist in all the cells.

Figs. 240—242. Independence of C from wing venation in *C. oedippus* F. In fig. 240 $C4$ and $C5$ are independent and located exactly in their cells; in fig. 241 they are fused and the fore end of the line of fusion deviates anteriorly from the 5th vein; in fig. 242 the same imaginary line passes from 4th cell into 5th one crossing obliquely the 5th vein thus $C4$ and $C5$ having lost their dependence upon the veins.

Figs. 243, 244. Independence of C from wing venation in *C. amaryllis* Cr. In fig. 243 $C4$ and $C5$ enter the 5th and 4th cells resp.; in fig. 244 they are fused and the line of fusion passes as in fig. 242.

Figs. 245—252. Dislocation in the ocellar series in *C. arcanioides* Pier. (figs. 245, 246), *arcania* L. (figs. 247, 248) and *dorus* Esp. (figs. 249—250). In fig. 245 $C6$ like its posterior homologues is attached to U; in fig. 246 $C6$ has migrated to M^1, in fig. 247 $C6$ has fused with M^1 and in fig. 248 has come to lie far from its 5th cell homologue. In fig. 249 the eye-spots of the 4th and 3rd cells are slightly shifted basifugally and basipetally resp., in fig. 250 and still more in fig. 251 the dislocations are more pronounced; in fig. 252 owing to these dislocations and the above dislocation of $C6$ the ocellar series consists of three parts which might be regarded as remnants of three parallel series but the above derivation. The flattened shape of $C5$ in fig. 251 due to its being pressed against E^3 is noteworthy.

Figs. 253—255. Wing-patterns consisting principally of eye-spots in *C. leander* Esp. (fig. 253), *C. symphyta* Ld. (fig. 254) and *C. nolckeni* Ersch. (fig. 255).

Fig. 256. Erebisation in *C. pamphilus* v. *lyllus* Esp. OC in the 5th cell is dislocated basipetally.

Figs. 257, 258. Characteristic combinations of OC in *C.* sp. (fig. 257) and *C. oedippus* F. (fig. 258).

Figs. 259—265. Coenonymphoid dislocation of M^1 in *C. pamphilus* v. *lyllus* Esp. (figs. 259—264) and *C. thyrsis* Frr. (fig. 265). M^1 is normal in figs. 259—260, it has displaced basipetally in 3rd and 4th cells in fig. 261, it has entered discal cell a little in fig. 262, more in fig. 263 and still more in fig. 264; a more pronounced condition of the intradiscal M^1 portion is seen in fig. 265.

Figs. 266—270. Coenonymphoid dislocation of M^1 in *C. arcania* L. In fig. 266 M^1 is distal to discal cell, it has entered the latter a little in fig. 267, more in fig. 268 and still more in figs. 269, 270.

Figs. 271—273. Tongue-like M^1 in *C. corinna* Hb. In fig. 271 M^1 forms tongue-like protrusion on the 5th vein which increases in fig. 272 and almost reaches OC in fig. 273.

Fig. 274. Oblique direction of M^1 in *C. thyrsis* Frr.

Figs. 275—283. Disappearance of M^1 in *C. amaryllis* Cr. In fig. 275 M^1 and light $U:M^1$ are normal, in fig. 276 $U:M^1$ has disappeared owing to darkening, in fig. 277 M^1 is shortened, in fig. 278 scarcely visible, in fig. 279 totally absent in forewing.

In fig. 280 $U:M^1$ is normal, in fig. 281 it is subdivided into $U:M^1$ and $U:M^1{}_1$, in fig. 282 the former has become $U:M^1{}_4$, in fig. 283 $U:M^1{}_1$ is absent, $U:M^1{}_4$ being the only remnant of $U:M^1$. Thus in fig. 279 M^1 is represented only by the small $M^1{}_4$.

PLATE VII.

Coenonympha and Triphysa.

Figs. 284—289. Disappearance of M^1 in *Coenonympha oedippus* F. In fig. 284 $U:M^1$ is light and broad, in fig. 285 it has darkened on forewing, in fig. 286 it is narrowed, in fig. 287 still more so, M^1 and C being in contact, in fig. 288 M^1 adheres C on hindwing, in fig. 289 M^1 is absent that being largely due to its fusion with C.

Fig. 290. *C. arcanioides* v. *marginalis* Btl. Pronounced light $U:M^1$ on hindwing, atrophy of M^1 on yellow forewing (OUDEMANS' phenomenon, see p. 256).

Fig. 291. *C. hero* L. Pronounced white $U:M^1$ and yellow iU on both wings (OUDEMANS' phenomenon, see p. 251).

Figs. 292—294. *Coenonympha iphis* W.V. $U:M^1$ is pronounced on both wings in fig. 292, shortened on forewing and divided into $U:M^1$ and $U:M^1{}_1$ in fig. 293, reduced to $U:M^1{}_4$ in fig. 294.

Figs. 295—297. *C. semenovi* Alph. In fig. 295 $U:M^1$ is wide, M^1 on hindwing forms four basifugal protrusions, in fig. 296 the latter begin to fuse with U, in fig. 297 the fusions are more pronounced and thus $U:M^1$ becomes subdivided into $U:M^1{}_{1.2}$, $U:M^1{}_{3.4}$ and $U:M^1{}_{6.7}$.

Figs. 298—303. *C. sunbecca* Ev., figs. 300 and 302 *sunbecca* v. *alexandra* Rühl. Prototypical M^1 in fig. 298, M^1, M^2 in fig. 301, vestigial eye-spot within $iU6$ in fig. 302, separate $iU6$ and $U:M^1{}_6$ in fig. 298, their fusion $(iU6 + (U:M^2{}_6))$ in fig. 301, considerable melanisation in fig. 299, and finally strong melanisation in fig 300 which reduces the interspaces to three series of markings (1) $iU6$, iU, iU_1, (2) $U:M^1$ and (3) $M^2:Bm_4$, $M^2:Bm_7$.

Figs. 304, 305. *C. mongolica* Alph. In fig. 304 $M^1 + M^2{}_4$ comparable to that present in *sunbecca* (fig. 303); in fig. 305 disappearance due to darkening of $M^2:Bm_4$ still present in fig. 304 and also, disappearance of M^1 from forewing.

Fig. 306. Prototriphysa. Explanation as in fig. 1.

Figs. 307—315 show principally the existence of the components of the prototype in the representatives of *Triphysa*.

Fig. 307. *Triphysa phryne* v. *dohrni* Z. General prototypical habitus.

Fig. 308. *T. phryne* v. *dohrni* Z. Pronounced E^1 and argentated E^3.

Fig. 309. *T. phryne* Pall. *OC* in 1st cells of both wings and E^1.

Fig. 310. *T. phryne* v. *dohrni* Z. Presence of U.

Fig. 311. *T. phryne* Pall. Presence of U.

Fig. 312. *T. phryne* Pall. Presence of M^2.

Fig. 313. *T. phryne* v. *dohrni* Z. M^1 in the 1st cell.

Fig. 314. *T. phryne* Pall. Presence of M^2.

Fig. 315. *T. phryne* v. *dohrni*. Presence of M^2. Some ends of its portions are bent basipetally along the existing ($M^2{}_7$, hind end of $M^2{}_4p$) or vestigial ($M^2{}_4a$, fore end of $M^2{}_4p$) nervures.

Fig. 316. *Triphysa phryne* Pall. Only 2nd *OC* present.

Figs. 317—320. Dislocation of *OC* in *T. phryne* v. *dohrni*. The series of *OC* is slightly bent s-like in fig. 317, the bend has increased in fig. 318 still more so in fig. 319 and resulted in a division of the series into anterior and posterior parts in fig. 320.

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THE WING-PATTERN IN PALAEARCTIC SATYRIDAE

PLATE VIII.

Triphysa.

Fig. 321. *Triphysa phryne* v. *dohrni* Z., fig. 322. *T. phryne* Pall. Modifications in M^1 and M^2. M^1 is distant from *OC* in fig. 321, approximated to them in fig. 322. $M^2 4$ in fig. 321 resembles $M^2 4p$ of fig. 315 being only more distended and forms a ring owing to the coalescence of its proximal ends in fig. 322.

Fig. 323. *T. phryne* Pall. Concave cell-portions of M^1.

Fig. 324. *T. phryne* v. *nervosa* Motsch. Pronounced melanisation, $M^1 1$, $M^2 1$ and $M^2 4$ evolve from their homologues seen in fig. 321.

Fig. 325. *T. phryne* v. *nervosa* Motsch. A still stronger melanisation than in fig. 324, the light marking in the hindwing discal cell derives from its homologue seen in fig. 324.

Fig. 326. *T. phryne* v. *dohrni* Z. Upperside.

In the *Argynnis* form of OUDEMANS' phenomenon (text-fig. 7, p. 222) the apical part of the forewing underside resembles hindwing underside, while the rest of the forewing underside resembles upperside. These relations are seen in figs. 33 and 34, 36 and 37, 39 and 47, 52 and 53, 97 and 98, 190 and 191, 202 and 205 and some others.

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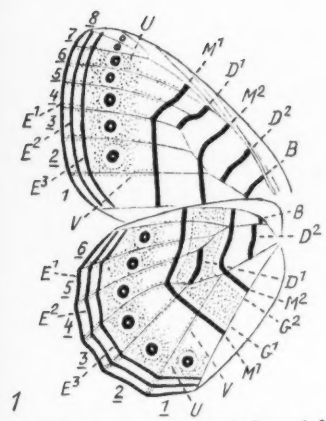

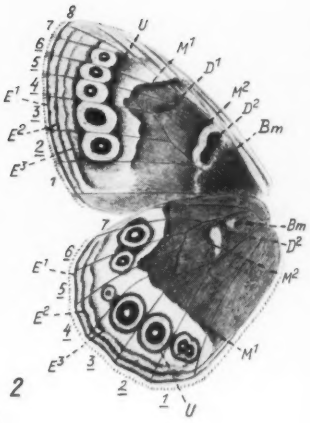

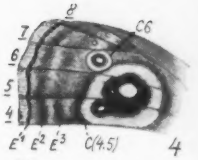

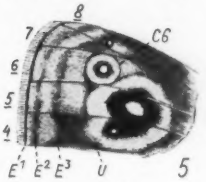

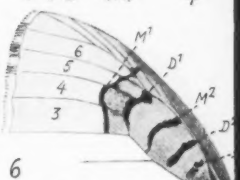

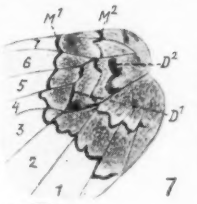

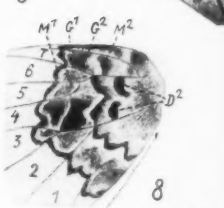

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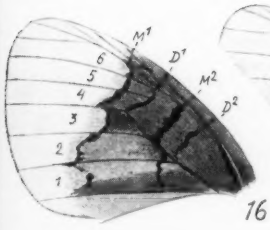

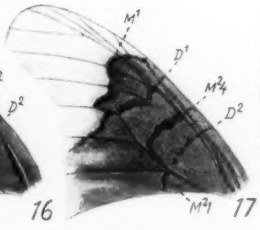

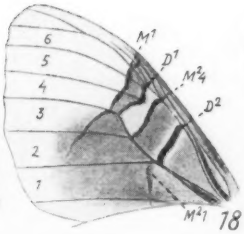

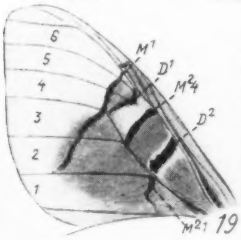

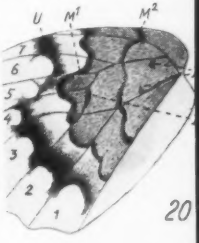

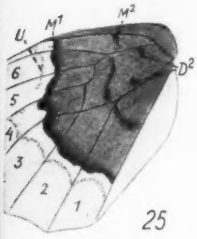

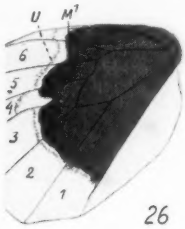

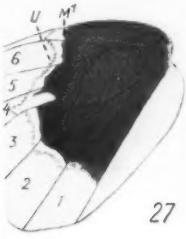

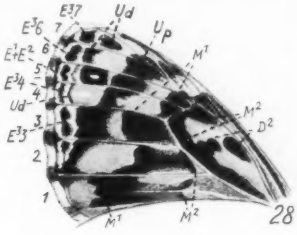

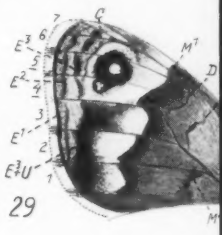

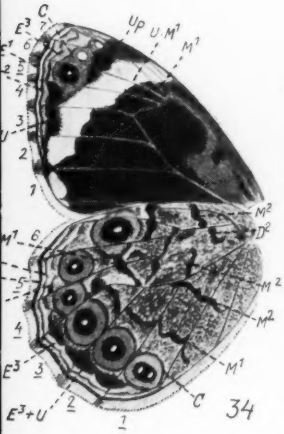

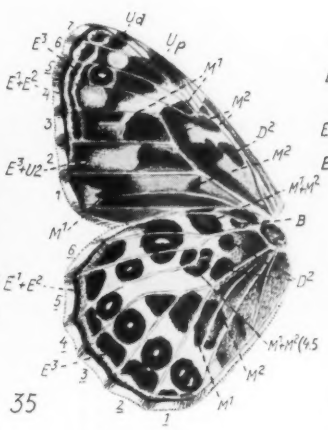

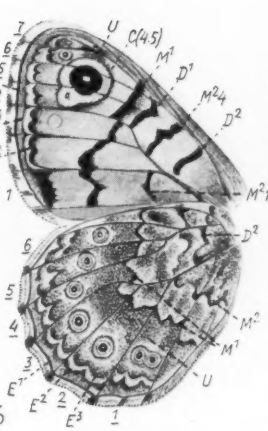

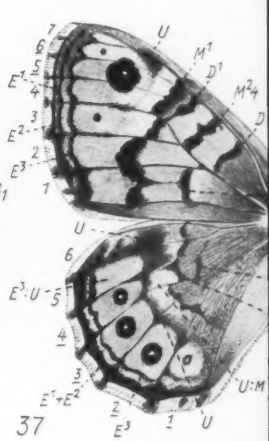

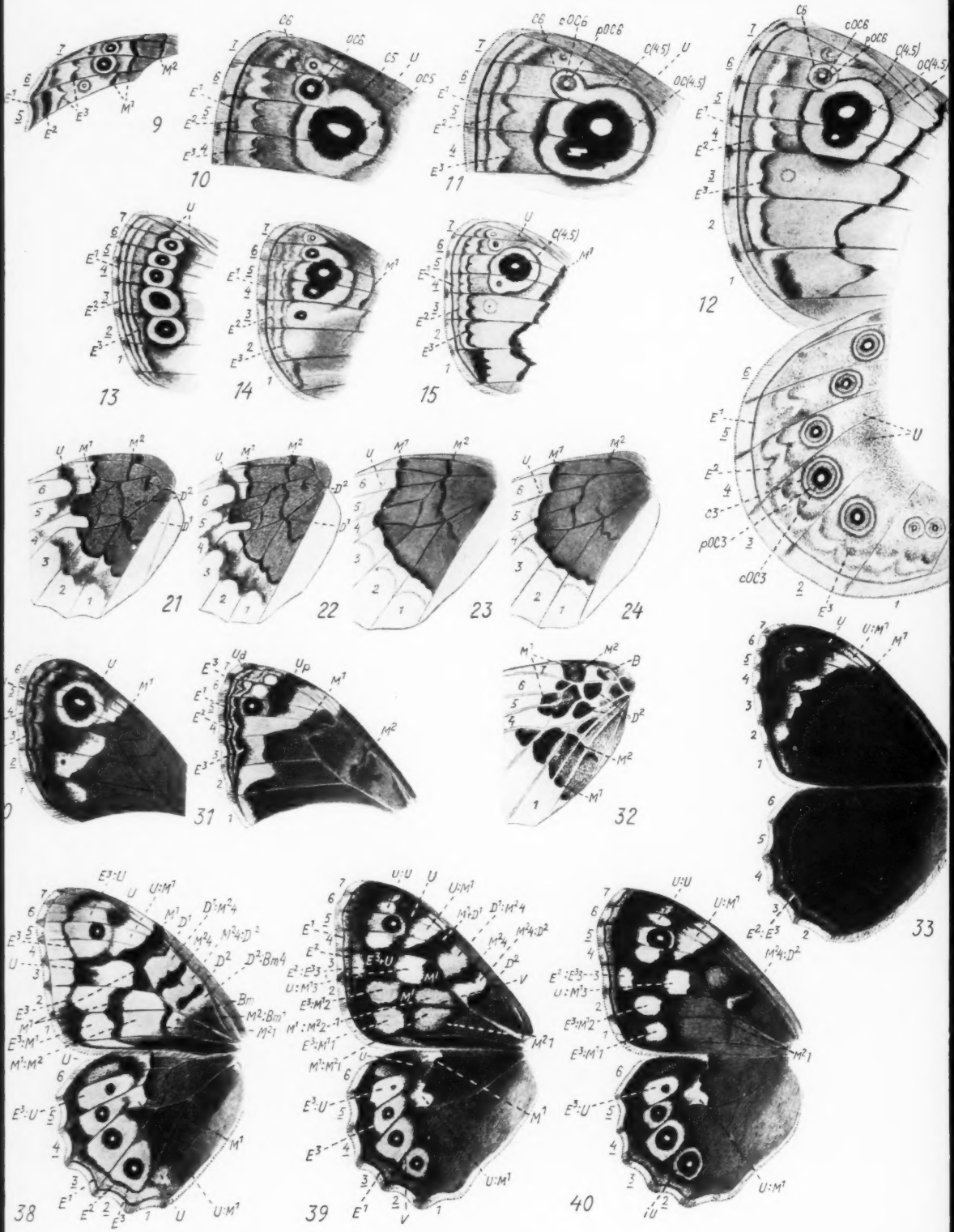

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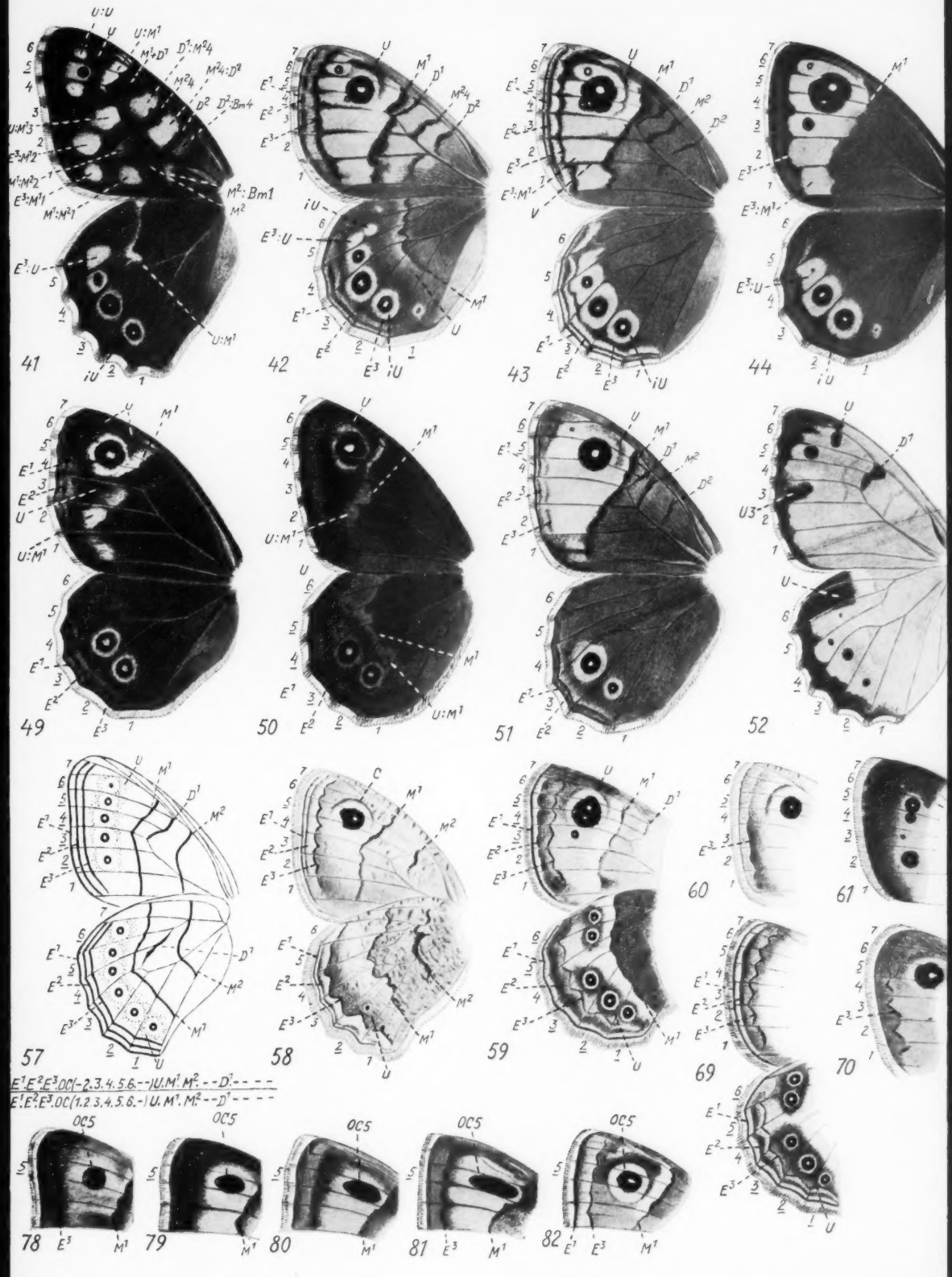
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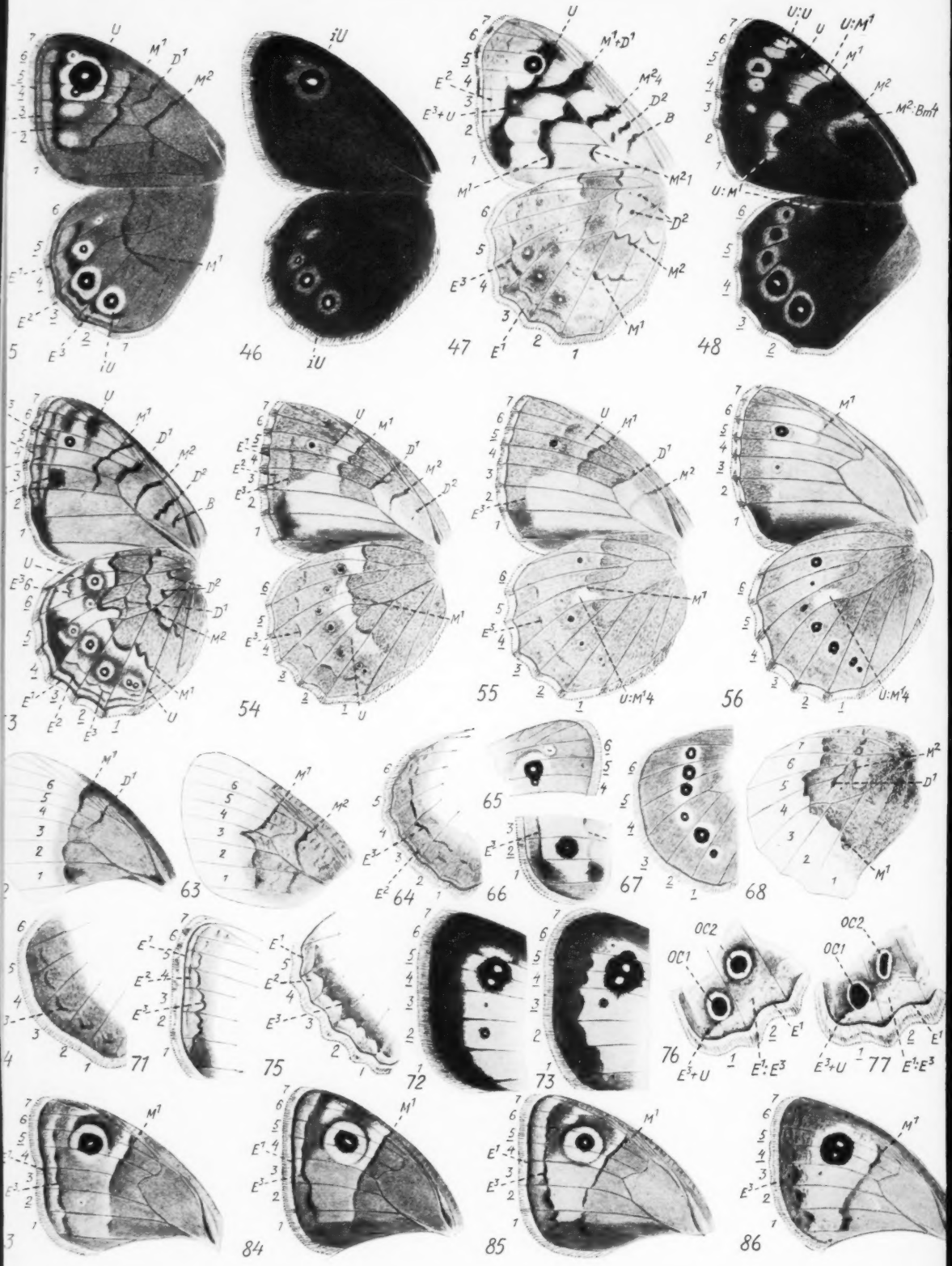

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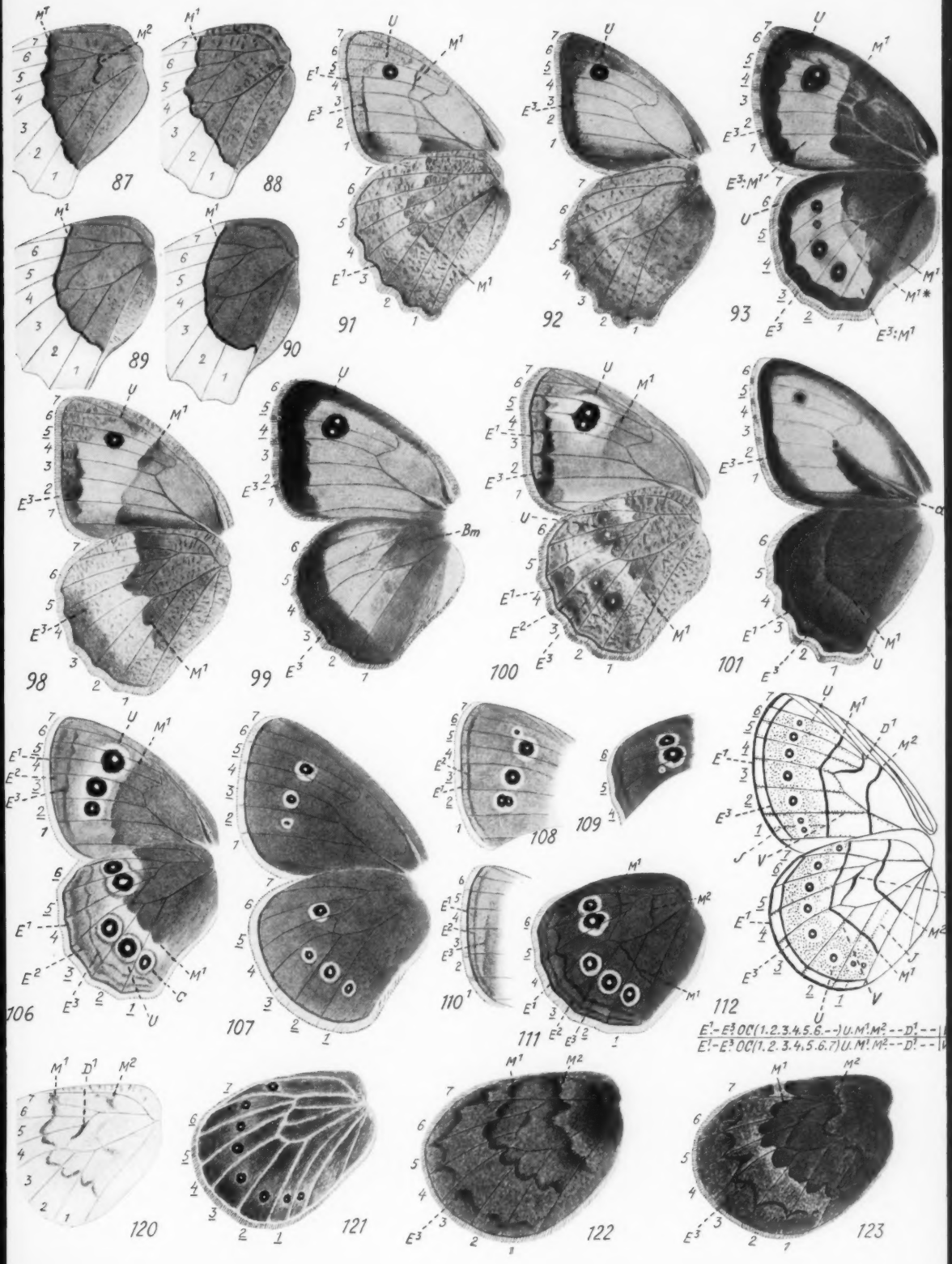
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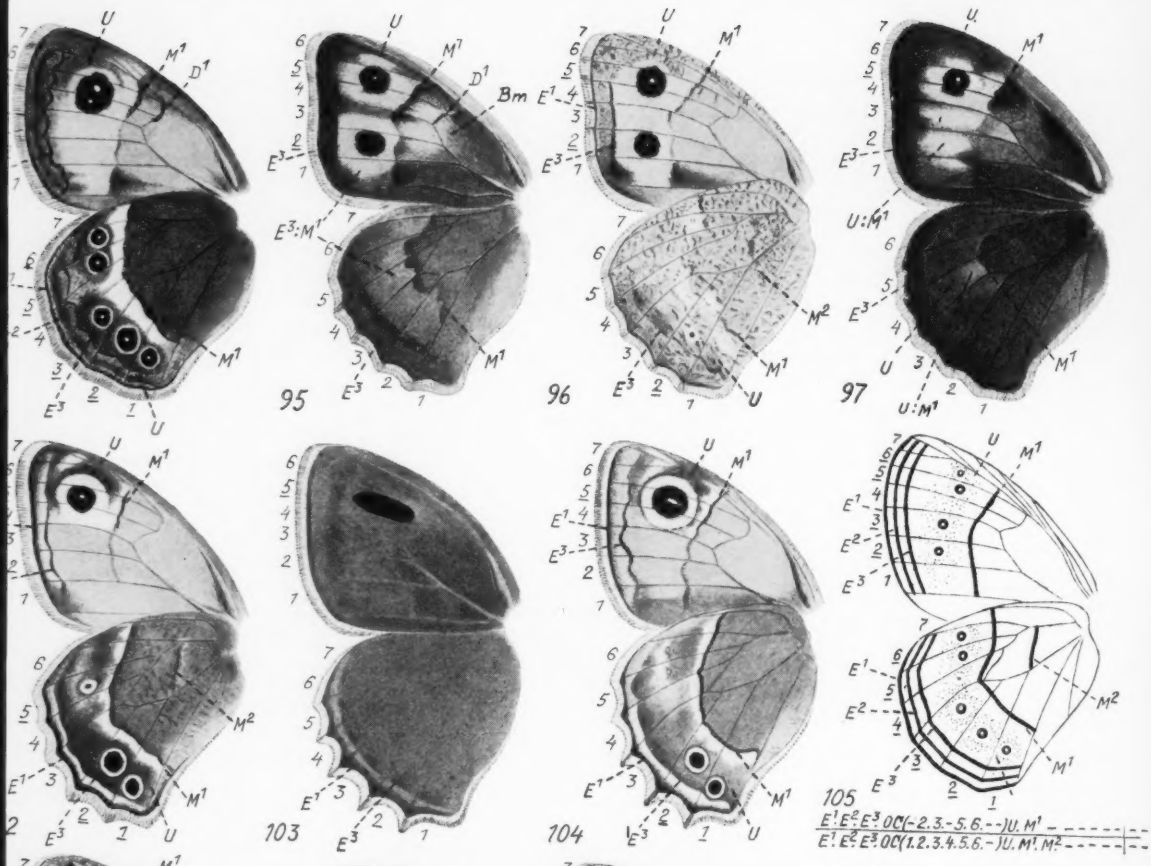
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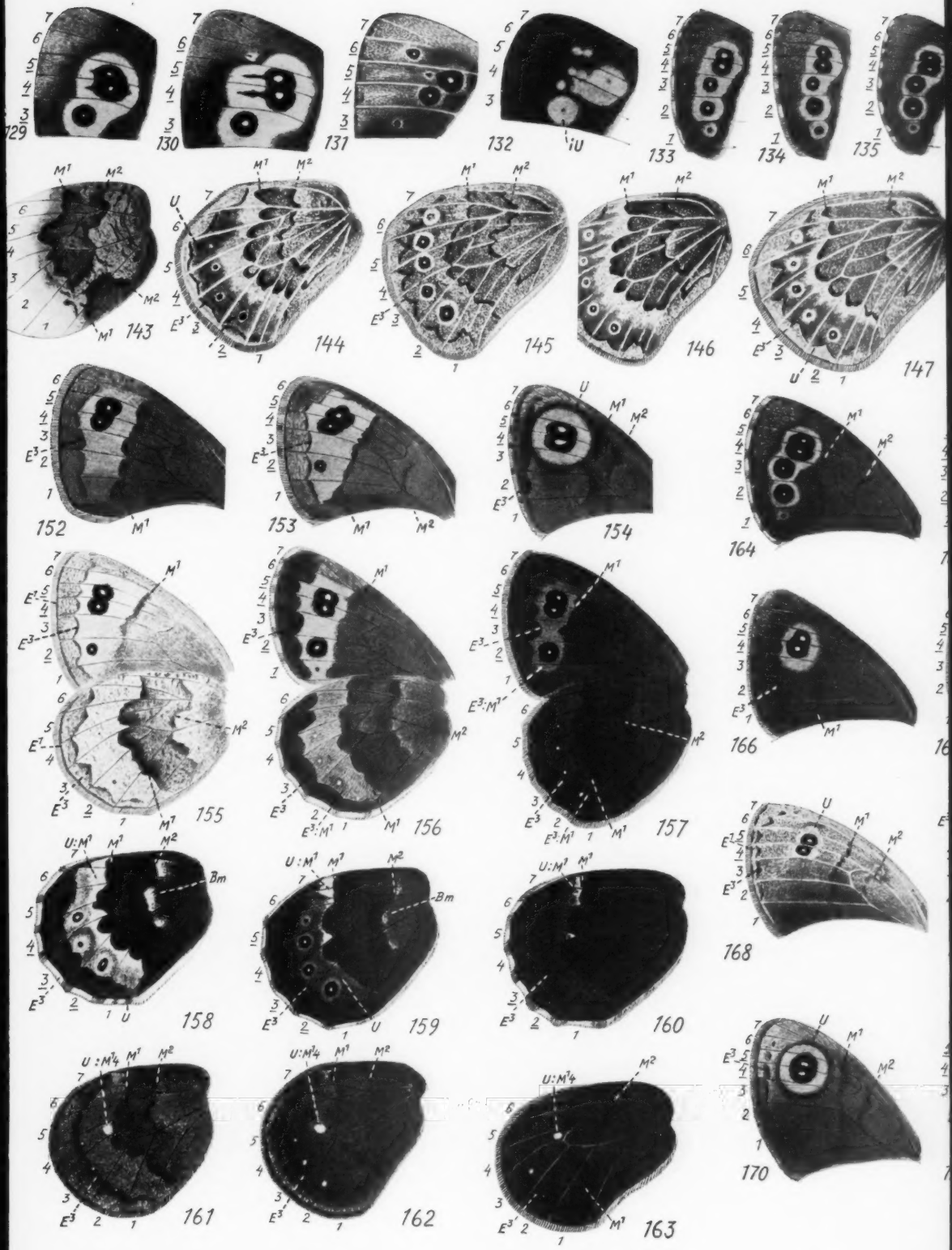
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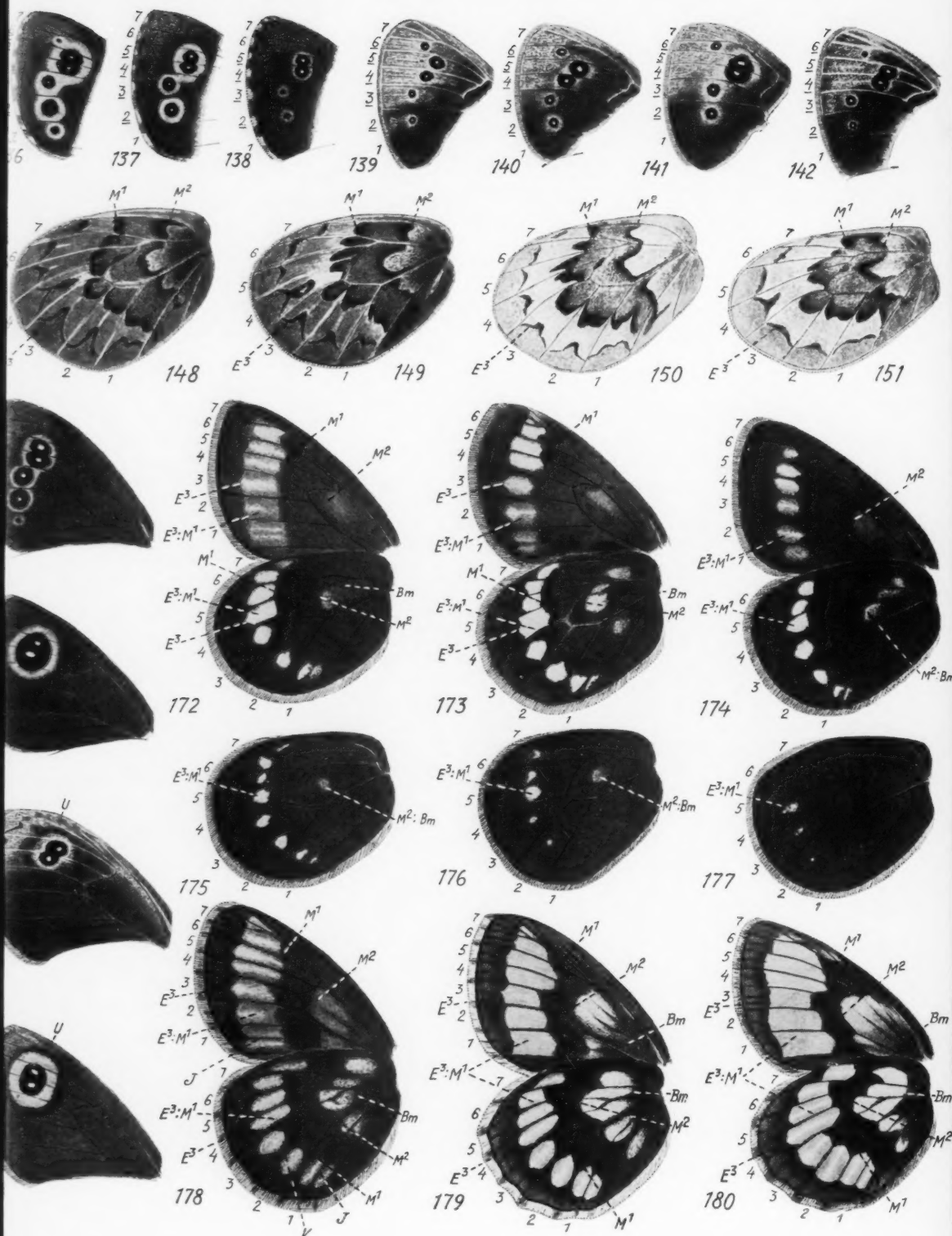
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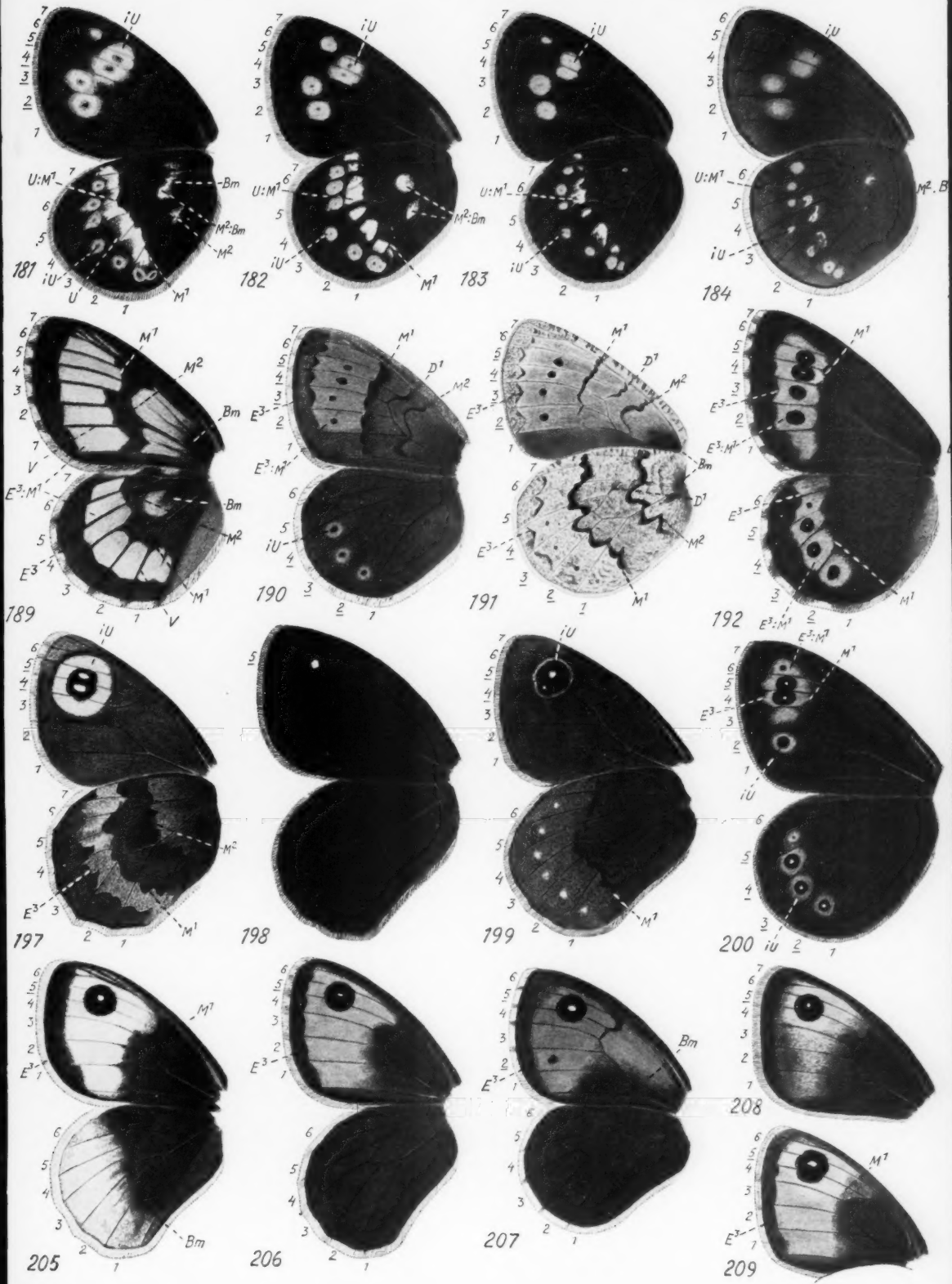
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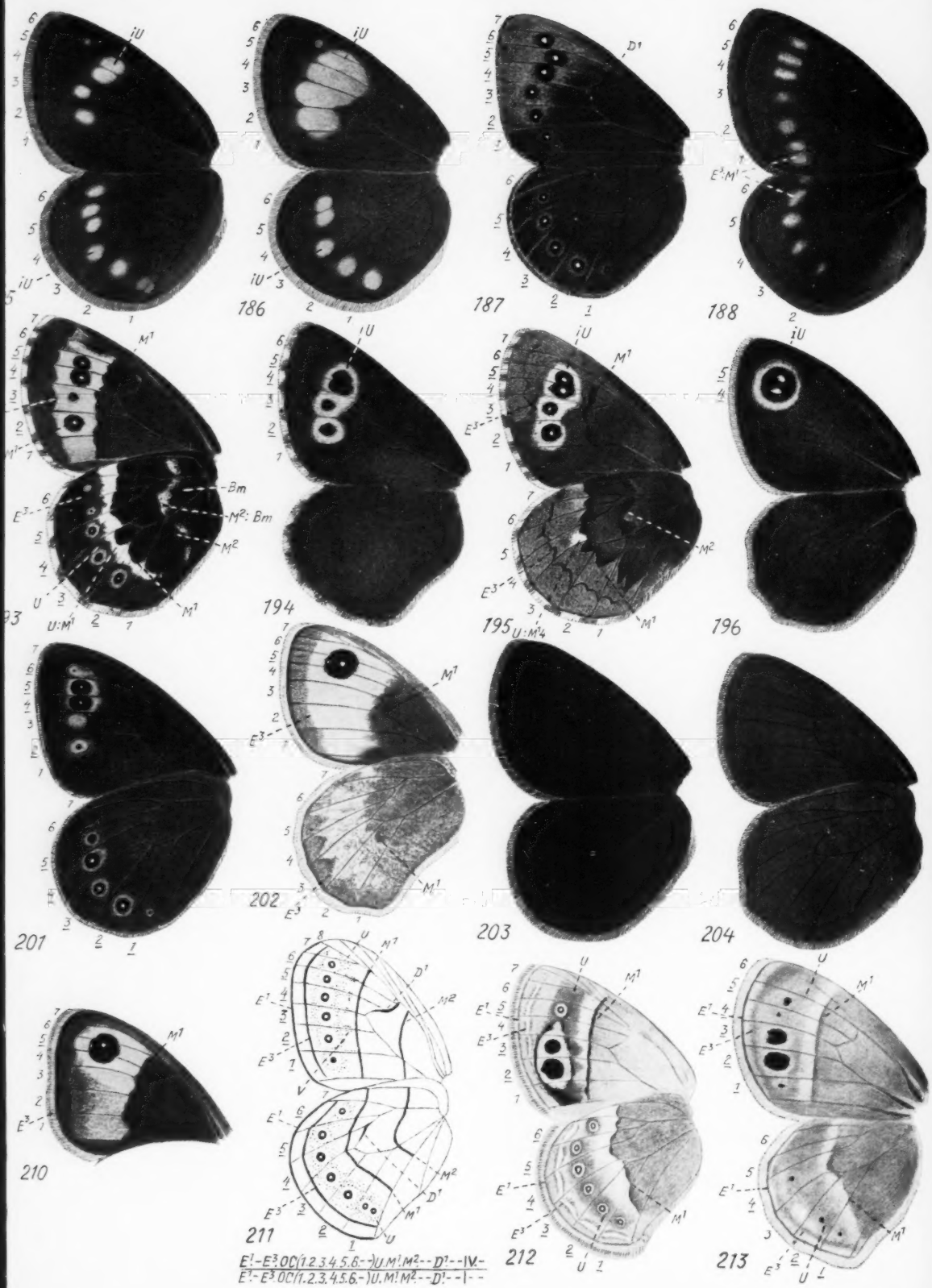
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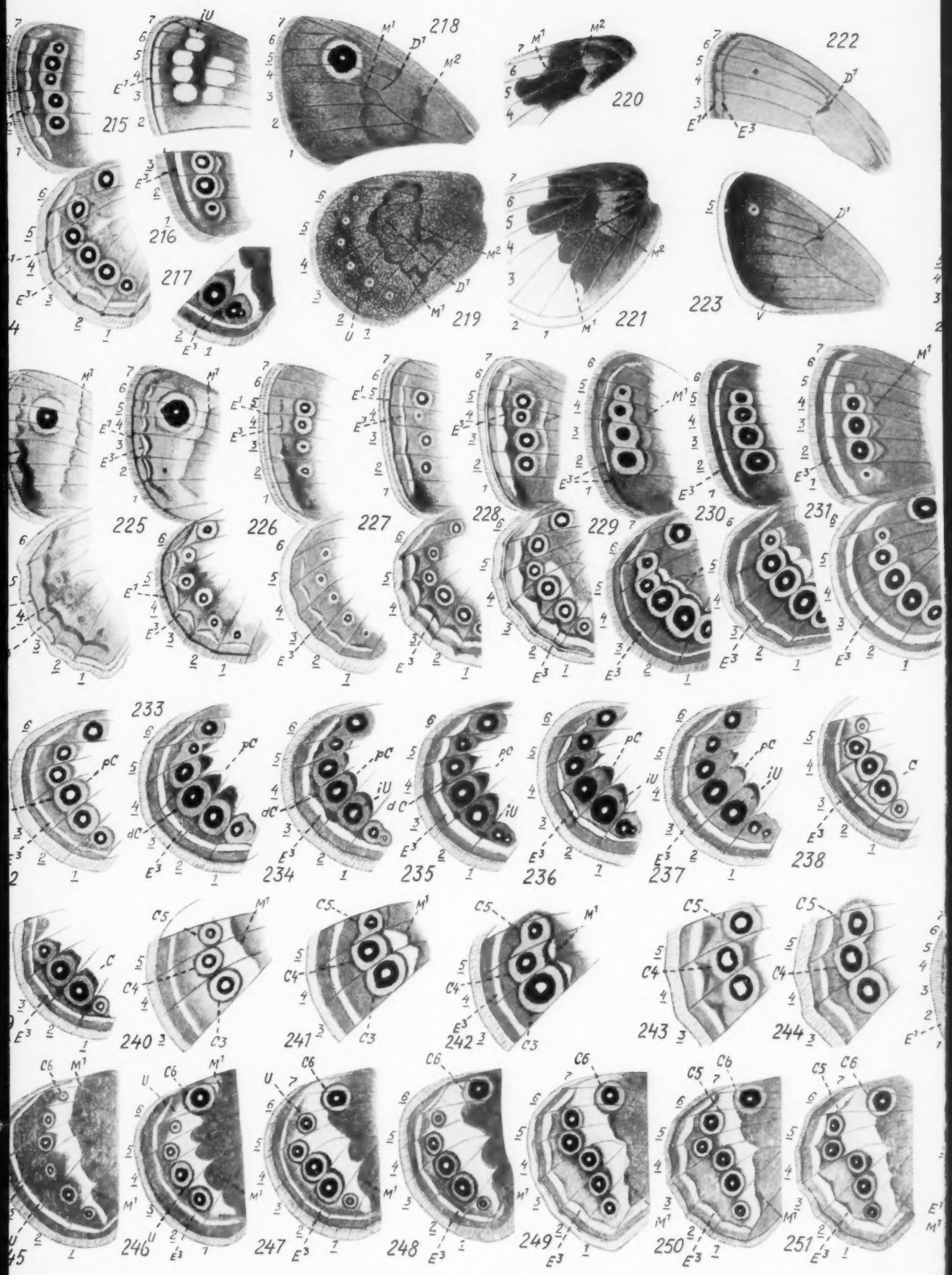
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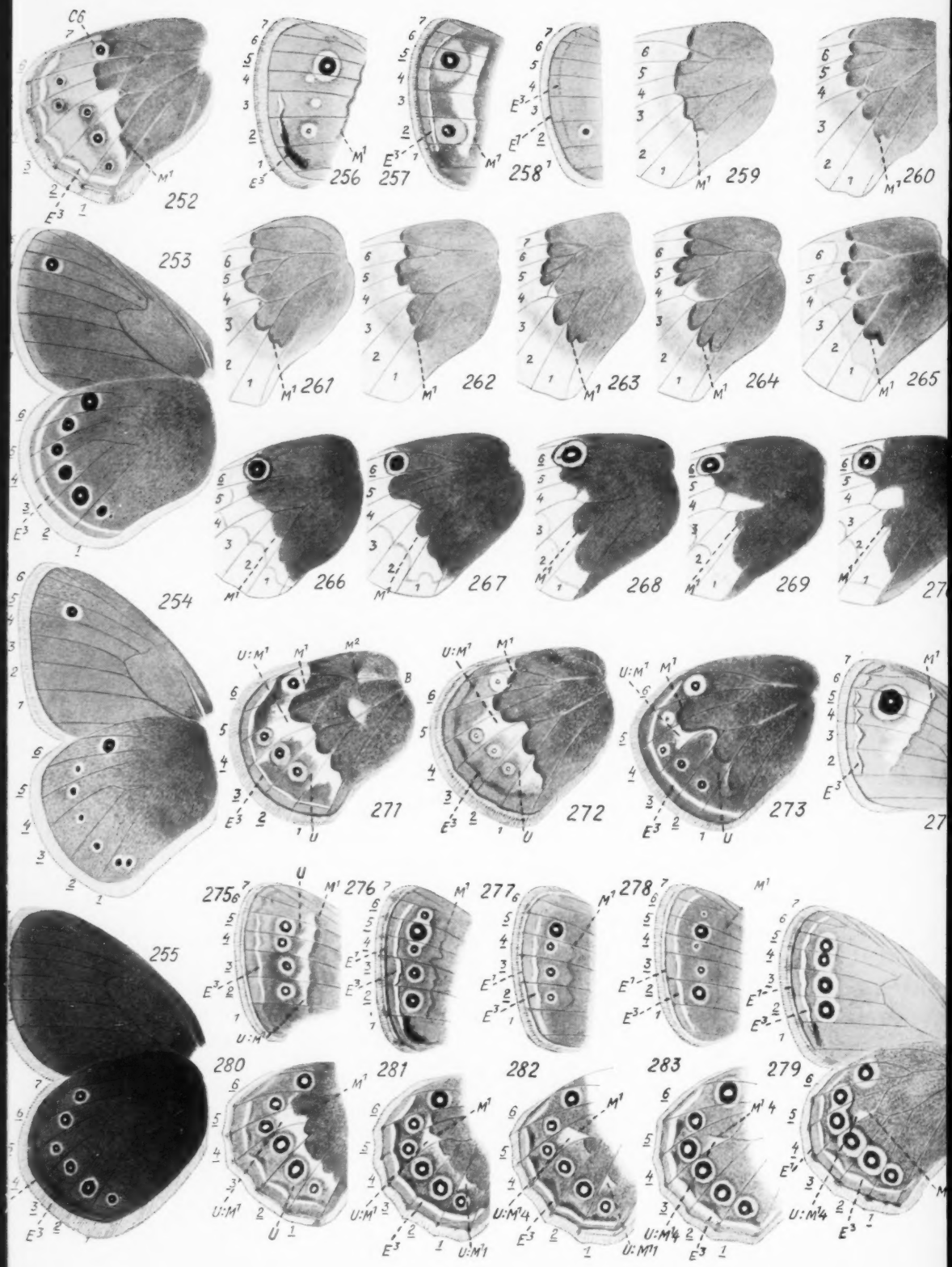
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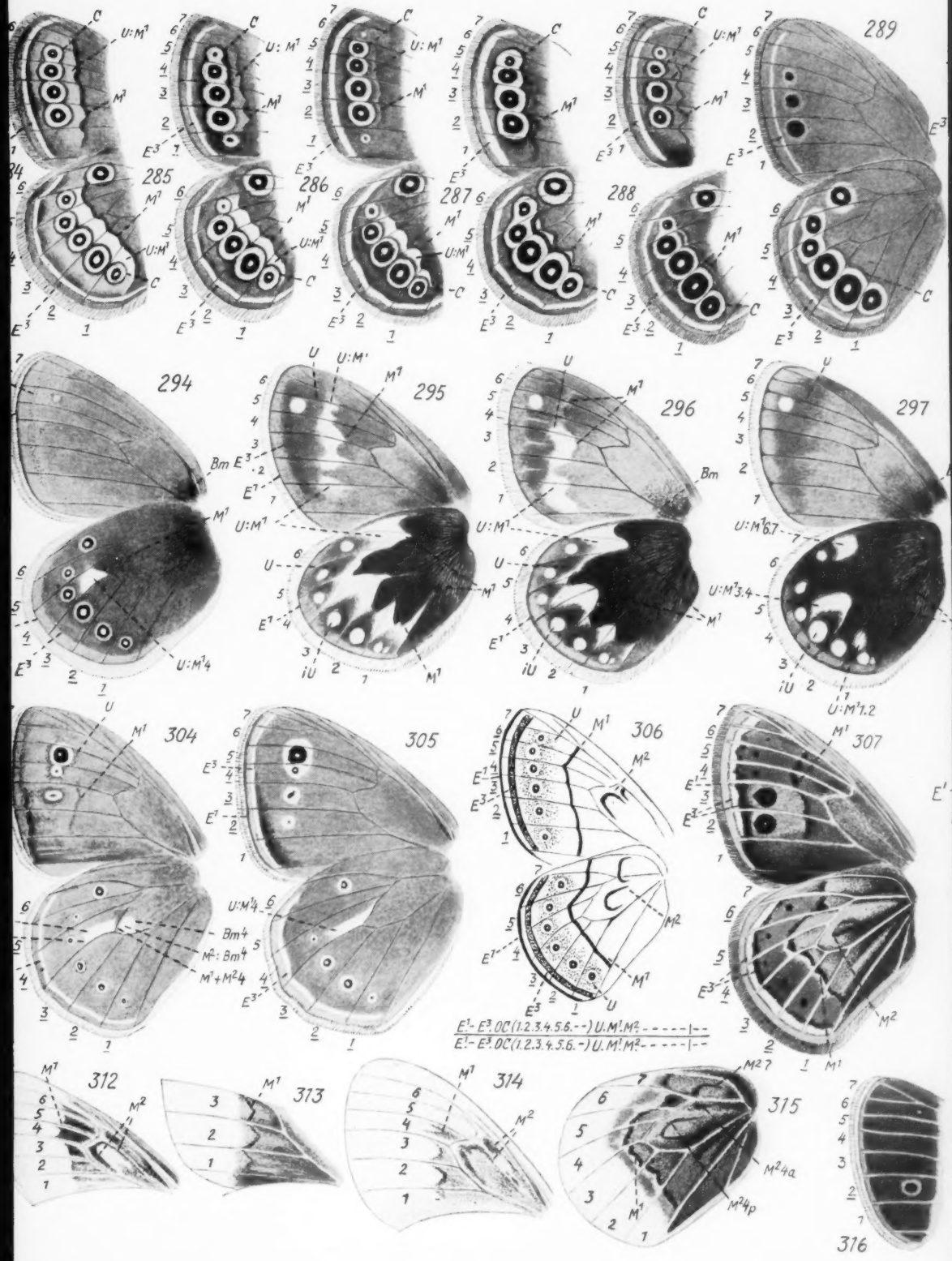
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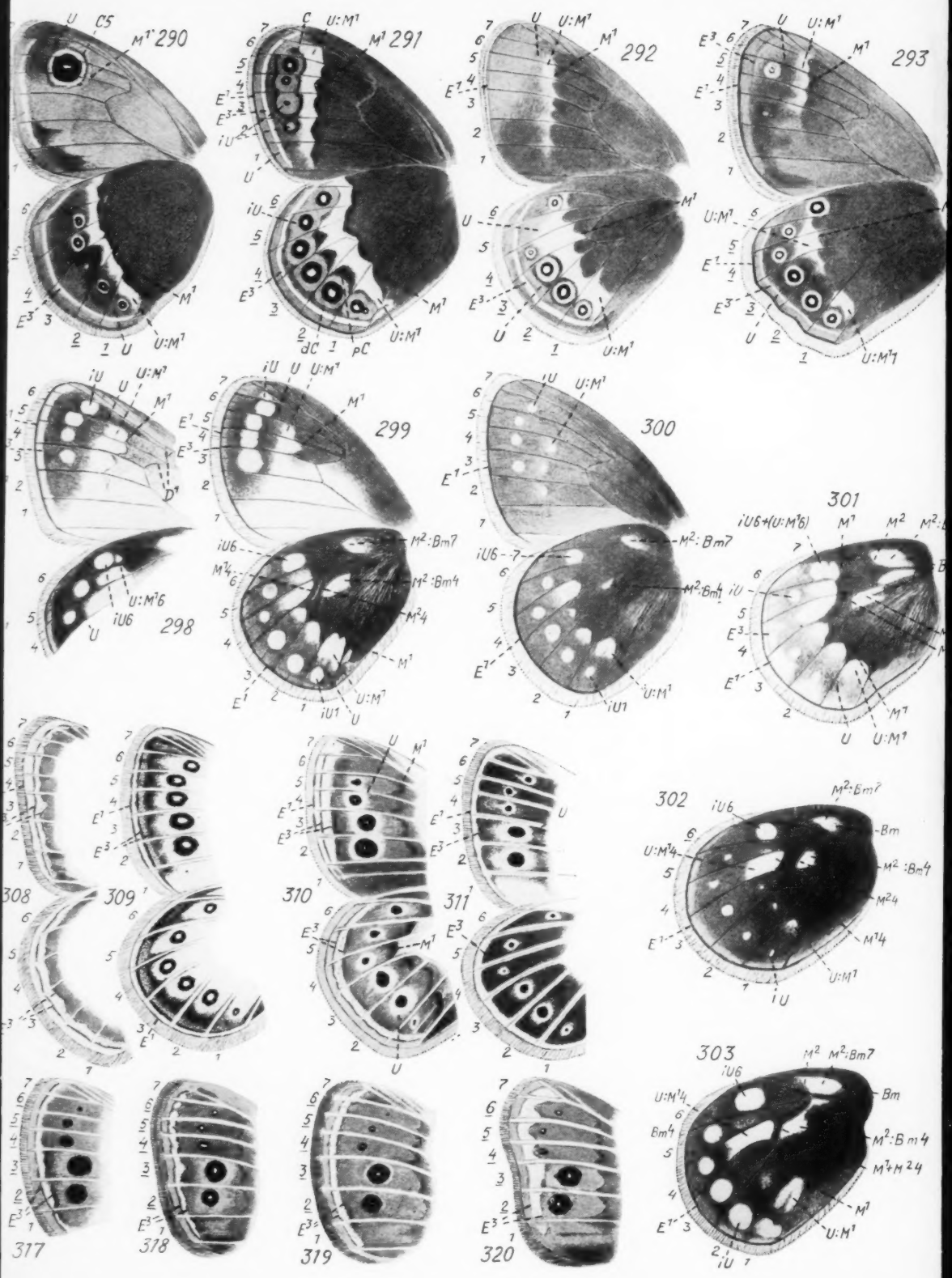
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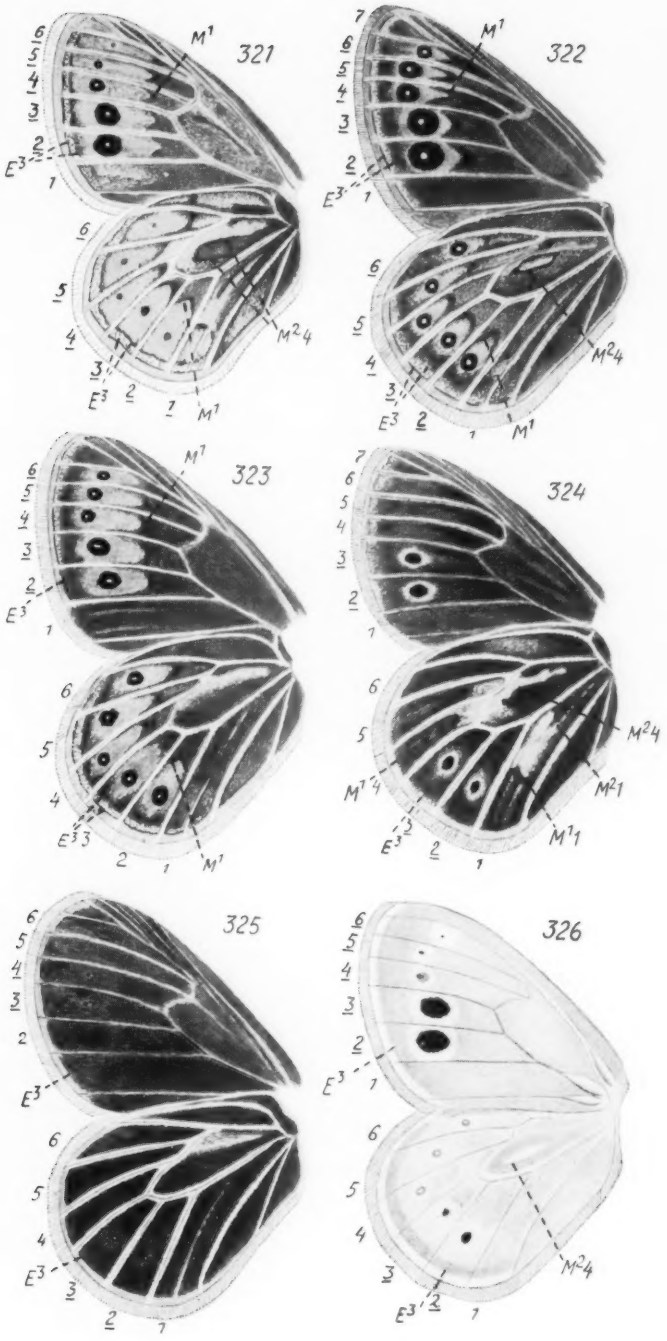
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A COMPARATIVE STUDY OF THREE NEW AMERICAN SPECIES OF THE GENUS PHAENOCORA WITH ESPECIAL REFERENCE TO THEIR REPRODUCTIVE ORGANS AND THEIR RELATIONSHIPS WITH THE OTHER DESCRIBED FORMS OF THE GENUS

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INTRODUCTION.

GRAFF, 1913, in his epoch-making review of the Rhabdocoela in "Tierreich", recognized eleven species of the genus *Phaenocora*: namely, *Ph. megalops*

Duges, 1830; *Ph. unipunctata* Örsted, 1843; *Ph. galiziana* O. Schmidt, 1858; Ph. *typhlops* Vejdovský, 1880; *Ph. baltica* M. Braun, 1885; *Ph. vejdovskýi* Graff, 1913 (= *Derostoma anophthalmum* Vejd., 1895); *Ph. gracilis* Vejdovský, 1895; *Ph. rufodorsata* Sekera, 1903; *Ph. anomalococla* Graff, 1913 (= *Anomalocoelus caecus* Haswell, 1905); *Ph. clavigera* Hofsten, 1907; *Ph. agassizi* Graff, 1911.

Among the eleven species mentioned above, the validity of *Ph. galiziana* has been questioned repeatedly because of it having been poorly described. Furthermore, the reproductive organs are said to lie posterior to the genital opening, which would be an unique position in this genus. However, NASONOV (1926) found specimens of *Phaenocora* in which the reproductive organs lie back of the genital opening as described for *Ph. galiziana* by O. SCHMIDT, but whose eyes lay away from the lateral edges of the body as in *Ph. megalops*. Earlier in the season he had found young specimens in the same ditch whose eyes lay at the lateral edges of the body in accord with O. SCHMIDT's description of *Ph. galiziana*. For this reason (which I confess is not at all clear to me) he has concluded that *Ph. galiziana* is not an independent species but a variety of *Ph. megalops*. On the contrary the above evidence leads me to conclude that *Ph. galiziana* is a valid species. Such a conclusion, however, can not be considered final without a carefully done, detailed study of the reproductive organs of both animals.

In the same paper, NASONOV states that *Ph. megalops* and *Ph. unipunctata* differ very little from one another (chiefly in the structure of the testes) and that he considers *Ph. unipunctata* to be merely a variety of *Ph. megalops*. In this conclusion, as in the previously stated one, I feel that he is not justified. If one will compare BRAUN's (1885) rather careful description of the reproductive organs of both *Ph. unipunctata* and *Ph. megalops*, it will be seen that they differ considerably in very fundamental structures (especially of their male copulatory organs). This matter will be considered in more detail in the body of this paper.

With reference to *Ph. anomalocoela*, however, I feel that there may be some question as to its validity as a Phaenocora-species. At best it appears to stand rather far removed from the rest of the species of this genus. HASWELL, 1905, in his very complete description of this animal, has failed to make mention of any pear-shaped appendages of the atrium superius, which are so characteristic of the genus *Phaenocora*. In addition to this, the configuration of the excretory organs is very unphaenocora-like.

Since GRAFF published his review of the rhabdocoeles in 1913, I have found recorded in the subsequent literature six new species and one new sub-species of *Phaenocora*: namely, *Ph. jucunda* Cognetti, 1914; *Ph. variodentata* Meixner, 1915; *Ph. vjatkensis* Nasonov, 1919; *Ph. achaeorum* Naso-

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nov, 1919; *Ph. typhlops subsalina* Luther, 1921; *Phaenocora* (*Megaloderostoma*) *polycirra* Beklemischev, 1929; and *Ph. beauchampi* Sekera, 1930.[1]; [2]

Among the above it would appear that at least three can at best be accepted only provisionally: *Ph. variodentata*; *Ph. vjatkensis*; and *Ph. achaeorum.*

According to Meixner (1915), *Ph. variodentata* has been described from two sexually immature individuals. It would seem rather illogical to accept unreservedly the above mentioned form as a new species without further study of sexually mature animals.

In regard to *Ph. vjatkensis* and *Ph. achaeorum,* it would seem that the former might easily be a subspecies or variety of *Ph. typhlops.* As a matter of fact, it appears from Nasonov's description to resemble *typhlops* much more closely than *Ph. typhlops subsalina* Luther, 1921 resembles the same. With reference to the latter (*Ph. achaeorum*), it would appear to be a new species. However, the structures described have been studied entirely from the living animal and have not been checked up by serial sections. While in some respects the study of the living animal is superior to the study of sections alone, I feel that a happy combination of the two is most valuable. Insomuch as the shape and position of the vesicula granulorum is so unusual for the genus *Phaenocora,* it would seem to be advisable to withhold judgment as to the validity of the species until such time as these features have been verified by serial sections. While Sekera's (1930) description of *Ph. beauchampi* is anything but complete, still the pseudoparasitic habits of this species sets it off from all other known forms of *Phaenocora.*

As far as *Ph.* (*Megaloderostoma*) *polycirra* is concerned Beklemischev (1929) has happily given a very complete description of this very interesting and remarkable animal. As Beklemischev points out, while it is so phaenocoran in many features, it is still so unlike *Phaenocora* in others, that he considers it should be placed in a new subgenus. Considerable further mention of this form will be made in the body of this paper.

In addition to the eighteen forms mentioned above, I wish to add three new American species. In my description of these forms I will endeavor to avoid going into the description of details of structure which are possessed in common by all phaenocoras with very little variation among the species. In doing this I will concentrate my attention on the fundamental structure

[1] Beklemischev (1927, pp. 193, 194) describes a form, *Ph. salinarum* (Gr), var. *subsalsa* nov., from the Bay of Odessa. Graff (1882) included this species, *Derostoma salinarum,* with the other *Derostoma*-species. Graff (1913), however, separated *Ph. salinarum* from the rest of the phaenocoras and placed it as *Derostoma salinarum* among the Rhabdocoelida dubia. Beklemischev wishes to refer it back again to the genus *Phaenocora* or at least to the Phaenocoridae chiefly on the structure of its yolk glands and male copulatory organ. His figure and description of the male copulatory organ, however, is not convincing. See discussion of male copulatory organs in this paper.

[2] Beklemischev (1919) also described another new species, *Ph. cucurbitina.* I have, however, been unable to get possession of a copy of his paper.

of the reproductive organs as being those structures that are most important from a systematic and phylogenetic standpoint. HOFSTEN (1911, p. 35) says most pertinently: "Das sicherste Erkennungsmerkmal liefert der männliche Copulationsapparat." I would like to put this in a somewhat different manner: namely, The structure of the male copulatory organ within sexually mature individuals of a given species is the least variable, consequently the most stable, character. Insomuch as it appears that it tends to vary least among the characters of a given species, it would seem reasonable to think that the degree of relationship between species can be most safely gauged by a careful comparison of the fundamental structure of their copulatory organs.

Several attempts have been made to place the species of the genus *Phaenocora* into groups that show a certain homogeneity. Among these has been the division into two groups, first by VEJDOVSKY (1895) and later defined by HOFSTEN (1911) as "Arten mit Augen und hinten zugespitzten Körper" and "blinde Arten mit hinten verbreiterten Körper". SEKERA (1904), on the other hand suggested that all phaenocoras with broadened posterior body and with a penis beset with thorns be placed in a new species, *Derostoma* (= *Phaenocora*) *dilatum*. It will be one of my tasks to endeavor to show that all such attempts to divide the genus *Phaenocora* into homogeneous groups has been entirely artificial, and I hope to give morphological evidence that in several cases there is closer relationship between two species of different groups than there is between either of these species and the rest of the species included within the groups in which they have been placed.

BENDL (1909) announced the presence of a ductus genito-intestinalis in *Ph. unipunctata* and demonstrated that it is a constant structure and not an abnormality. Since then it has been described by COGNETTI de MARTIIS (1916) for *Ph. jucunda* and by LUTHER (1921) for *Ph. typhlops*. It was also mentioned by BEKLEMISCHEV (1929) as being present in *Ph.* (*Megalodcrostoma*) *polycirra*. MEIXNER (1915) mentioned it as probably being present in his *Ph. variodentata*. STEINBÖCK (1924) advanced his theory that the ductus genito-intestinalis, or more properly speaking the "Geschlechtstrakt-Darmverbindung", arose as an evagination of the gut and formulated a terminology for the description of its derivatives. In that the derivatives of the "Geschlechtstrakt-Darmverbindung" differ markedly among my three species —apparently showing different levels of the evolution of these structures— I am also including in this paper a comparative study of these structures.

Though much has been written with reference to the pear-shaped appendages of the superior genital atrium of *Phaenocora*, and while BEKLEMISCHEV (1929) says with reference to these appendages in his species: "Beim jungen Tiere stellen die Uteri feste ovale Körperchen vor, deren Struktur daran nicht zweifeln lässt, dass sie mit den paarigen zelligen Anhängen der übrigen Phaenocora homolog sind," yet I feel that there still may be much to be

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learned with reference to these structures and I think considerable evidence can be adduced to support the opinion that these structures are primitive and not vestigial in the *Phaenocora*-species, and I hope to make some observations that may throw further light on these structures.

KNOWN OCCURRENCE OF PHAENOCORA IN THE UNITED STATES.

GRAFF (1913) listed under the "Phaenocorinorum species dubiae" a form, *Derostoma elongatum* Schmarda, 1859. This form, which was 2 mm. in length and without eyes, was collected in the brackish waters of a swamp near New Orleans. I have tried to obtain SCHMARDA's original work, but have been unable to do so up to the present time. In all probability, however, the description is entirely inadequate.

In 1911, GRAFF described a form, *Phaenocora agassizi,* which he found in small numbers in the sediment of a pool at the "East wide waters" (at the end of Ericsson Street), Rochester, New York. The older animals of this species were 1.5—2 mm. in length, possessed eyes, and the epidermis contained rhabdites. The possession of dermal rhabdites, while apparently not occuring in the European species, occurs not only in *Ph. agassizi* but also in my new species, *Ph. virginiana, Ph. kepneri,* and *Ph. highlandense,* as well as in the Australian form *Ph. anomalocoela* GRAFF described the body as being milk-white. This of course would indicate that they did not possess zoochlorellae. This condition, however, may have been incidental or seasonal, as I have often found white individuals among my specimens which usually possess zoochlorellae. I have been very anxious to obtain some specimens of this species as GRAFF's description is incomplete in many respects and his description and drawings of both male and female reproductive organs do not fall in line with what I would expect to find in a phaenocoran. I was, however, unable to do so, as I found out (through the courtesy of the University of Rochester) that the "East wide waters" which was a part of the old canal system, now discontinued, has been drained and is now a subway station of city's electric street railway lines.

The next mention that I found of an American *Phaenocora,* was made by MACARTHUR (1921) who carried on experiments in gradients in vital staining and susceptibility in several forms including *Phaenocora.* MACARTHUR referred to the form as *Ph. agassizi,* but on communicating with him I found that he had not identified the species as he was interested entirely with the physiological aspect of his work. Dr. MacArthur referred me to Dr. Libby Hyman who was at the University of Chicago at the time he carried on his experimental work with *Phaenocora* at that institution. I received an extre-

mely courteous reply from Dr. Hyman telling me that she thought Dr. MacArthur got his specimens from material collected in the neighborhood of Pine, Indiana, about 20 miles southeast of Chicago. Dr. Hyman said that she saw the Phaenocora many times in cultures of pond material but does not remember it well enough for specific identification but is under the impression that it possessed rhabdites.

During the spring of 1927 and the fall of the same year, a large number of phaenocoras was found in pools and streams in the vicinity of the University of Virginia. These animals were from 0.7 mm. to 1.3 mm. in length, with reddish eyes, heavily pigmented about the eyes and pharynx, and usually dark green through the presence of zoochlorellae. In the following spring (1928) a few specimens were collected but not in as large numbers as during the previous year. During the above-mentioned period, J. S. CARTER (1929) made some observations on this species relative to the effect of different kinds of food on the length of life of these animals, time required for the development of the egg, etc. In this paper CARTER refers to this form as *Ph. agassizi,* supposing it to be the same species as that described by GRAFF (1911). During the months of May and June, 1929, five specimens were collected from the reflection pool by the Gymnasium. These examples were fixed and sectioned. Some time in June of the same year (1929) Dr. William Kepner made a sketch of the everted penis of this animal and realized that these animals could not be referred to the species *agassizi* as described by GRAFF (1911), as the penis proved to be entirely unarmed in contrast to the thornlets exhibited by GRAFF's species. However, no serious attempt was made at that time to identify this form as one of the known European species or to establish it as a purely American form. During the following year (1930) quite a large number of specimens were collected in the vicinity of the University of Virginia, most of which were taken from the reflection pool and the old University reservoir. In the fall of the same year I found large numbers of these animals in material collected from an artificial pond on the Lynchburg road, at a point about three miles south of the University. This pond is used for the rearing of game fish for the re-stocking of the local waters and was drained the next spring and has been drained repeatedly since then. I have repeatedly collected material from this locality since the pond was drained the first time and at no time have I again found a single *Phaenocora.* During the summer of 1931 these animals became extremely rare and throughout the year of 1932 not a single one was found. Fortunately sketches had been made of the living animals and a large amount of prepared material was at hand, both in the form of serial sections and of total mounts. In February of this year (1933) I obtained a single specimen from a collection made at the old University reservoir. In examining this specimen in the living condition under the microscope, I inadvertently subjected the cover-

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glass to undue pressure in order bring out the details of the reproductive organs, as this animal was unusually opaque due to the presence of great numbers of zoochlorellae. The excessive pressure on the cover-glass resulted in a rupture of the body wall in the region of the pharynx. To my great surprise I saw several colorless euglenoid forms emerge from the point of rupture. By more careful observation I was able to see that the whole pseudocoele of the animal was literally alive with similar forms. HALL (1931), while working at the Miller School of Biology, University of Virginia, described a colorless euglenoid parasite, *Euglena leucops*, from the pseudocoele of *Stenostomum*. This form is described by HALL as possessing a stigma, and by having the ability of elaborating a flagellum when outside of the host. As far as I was able to observe, the euglenoid parasite of *Phaenocora* possesses neither stigma nor flagellum and in these respects would appear to agree with the euglenoid form reported by HASWELL (1892) as a parasite of an undetermined Australian rhabdocoele. Whether the apparent progressive disappearance of this form from our local waters is due to the effects of this parasite is a matter for conjecture.

On April 19, 1931, Dr. William Kepner found in material which he had collected at Marsh Creek, Adams County, Pennsylvania, near "Black Horse Tavern", a *Phaenocora* which differed markedly from the one mentioned above. These animals were from 2 mm. to 2.5 mm. in length with blackish eyes, pigmentation practically wanting, the body while considerably longer than in the local form was much slimmer in proportion to its length, pharynx more elongated, the body while often green with zoochlorellae never showed the dense green color often exhibited by the local form, and like the preceding form also possesses dermal rhabdites. This Pennsylvanian form proved to be easily cultured and was fed *Dero* and beef liver with great success. On subsequent occasions more material was collected from the same locality and cultures were maintained in the laboratory until the summer of 1932.

On May 15, 1931, Mr. Threlkeld of the Department of Zoology at the Virginia Polytechnic Institute, Blacksburg, Virginia, sent to this laboratory some examples of *Phaenocora* which he had collected from a pool on the campus of the institute. Later on I found these forms to be identical with the forms found at Marsh Creek. Mr. Threlkeld has very kindly sent further specimens from this locality from time to time.

On October 26, 1931, Miss Margaret Hess brought me several phaenocoras which she had taken from material collected from a spring branch of the Bull Pasture River at a point about four miles south of the village of Mac Dowell, Highland County, Virginia. This locality is about 90 miles northwest of the University, with an altitude of about 650 meters, in contrast to the altitude of something less than 200 meters at the University. These animals proved to be considerably larger than either of the before-mentioned forms,

being from 3 to 3.7 mm. in length. The body while long was relatively stout, the pharynx relatively short and broad, the eyes reddish in color, the anterior end colored a rich red as far back as the posterior edge of the pharynx where the color graded off insensibly into the color of the body proper. These animals, like both the other forms mentioned above, were usually colored green by the presence of zoochlorellae and possess dermal rhabdites. In November of the same year (1931), Miss Hess brought me more of these forms, which, however, I was unable to culture successfully over a long period of time. During the following summer (1932), however, I visited this locality, which is situated in a beautiful mountain valley, and succeeded in collecting large numbers (100 or more) of these forms.

It is worthy of remark that while the triclads seem to be represented in America by species that are peculiar to America only, the rhabdocoeles are often represented by species which are common to both the European and American faunas. While it is probably true that some American rhabdocoeles which have been referred to European species will, under further investigation, prove to be purely American species, still there are unquestionably many rhabdocoeles represented in the American fauna which are identical with forms already described for Europe. The three new species which I will describe in the body of this paper differ considerably from any hitherto described forms. While these forms appear to be purely American, there seems to be no good reason why these species should not eventually be found among the members of the European fauna.

I have named the first-mentioned form, found in the vicinity of the University of Virginia, *Phaenocora virginiana*. The second form, found at Marsh Creek, Adams County, Pennsylvania and at Blacksburg, Virginia, I have named *Phaenocora kepneri* in honor of my friend and teacher, Dr. William Kepner. The third form found near MacDowell, Highland County, Virginia, I have named *Phaenocora highlandense*.

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TECHNICAL PROCEDURE.

The study of serial sections alone is an unsatisfactory method of making an accurate morphological investigation of the rhabdocoeles. The process of fixation causes not only a shrinkage of the individual cells — the extent of the shrinkage depending more or less on the fixing fluid used — but the whole morphological relationship exhibited by the organs themselves to one another may be, and most usually is, very greatly deranged. It is therefore necessary to supplement the study of serial sections by a careful study of the living animal. Even this method has its limitations, as the pressure necessarily exerted on the cover-glass in order to distinguish the anatomical details of the

various organs, often produces a distortion of the same both as to their position and to their form. I have therefore made it a practice to make a preliminary investigation of the living animal without restrictions imposed by a cover-glass in an endeavor to map out, in the unrestrained condition, the outline of the animal and the position of such organs as can be observed in this manner. After the preliminary study of the animal has been made and the proper points of orientation established, the animal was studied under a cover-glass supported by a ring of vaseline. Any desired amount of pressure can be exerted on the animal so confined by pressing carefully on the cover-glass. The ring of vaseline also serves to keep the animal from drying out. The study of the living animal and serial sections was further supplemented by the study of total mounts which were stained by various dyes. These mounts were of two kinds: those that were prepared by killing and fixing the animal under the restraint of the cover-glass and those in which the animal was killed and fixed while swimming freely in a few drops of water. In the latter case every effort was made to kill and fix the animal in the extended condition, either by first killing with a weak solution of nitric acid and then fixing, or by the use of a hot fixing fluid. Such a specimen is stained and then mounted under a supported cover-glass in order to prevent crushing, and proved very useful in the study of the shape and extent of the testes, yolk glands, etc.

For the killing and fixation of the material used in this study, several fixing reagents were employed: namely, Goldschmidt's; Zenker's; sublimate; and Beauchamp's. Of these Beauchamp's (alcohol-formol-glacial acetic acid) proved in many ways to be the most satisfactory in that it caused little shrinkage of the cells. The result was a natural picture of the organs and their relationship to one another. The animals when killed by Beauchamp's fluid do not contract to the extent that they do when killed by other fluids used. It has one great drawback, however, as it practically destroys the epithelium, as the large amount of acetic acid used in its composition reacts with the dermal rhabdites and the contents of other epidermal glands, resulting in the production of gasses which literally blow the epidermis into shreds. The staining qualities of the tissues fixed by it are, however, excellent and the natural appearance of the internal organs makes it an extremely satisfactory reagent for the fixation of these animals in which the study of the reproductive organs is of the first importance. Zenker's fluid, on the other hand, proved to be an excellent reagent for general use both for total mounts and for serial sections. The epidermis was well preserved but the amount of acetic acid, while not great enough to destroy the epidermis, was still large enough to discharge the rhabdites when present. The cell contents were well preserved by this fluid but considerable distortion took place, even when used hot. A saturated aqueous solution of sublimate to

which had been added four or five drops of glacial acetic acid to 200 cc of the solution did not in any way destroy the dermal rhabdites but considerable shrinkage of the cells took place resulting in some distortion of the organs and the loss of the crisp cell outlines so characteristic of material fixed by Beauchamp's fluid. When used hot, or when the animal was previously killed by very dilute nitric acid, the distortion was less evident but the individual cells still showed considerable shrinkage. However, I have several series of sections killed and fixed in this manner which are quite satisfactory but in the cases in which nitric acid was used for killing, the dermal rhabdites were wanting.

For the staining of the total mounts, Delefield's haematoxylin, alum cochineal, and borax carmine were used. Of the three, I believe the last gave the best results as this stain, when properly used, is very transparent. Delefield's haematoxylin and eosin, and Mallory's triple stain were used almost exclusively for the staining of serial sections. I found Mallory's triple stain especially useful and I used it for staining material fixed by all of the above-mentioned fixing fluids. The color pictures after Zenker's and sublimate are practically identical; the staining results after Goldschmidt's differs very little from results after using either of the above; but the color picture resulting after Beauchamp's fluid differs in many respects from the results achieved after using any of the former fluids. As a matter of fact, I found it necessary to add a small amount of dilute hydrochloric acid to the acid fuchsin solution before I could get the muscle fibers to take the stain at all. After doing this, however, the results were remarkable, as the muscle fibers stood out very sharply in a manner only rivaled in material stained by iron haematoxylin. There were other changes in the color picture, however, such as the staining of the contents of certain glands a bright blue that were stained a bright red when the tissues had been fixed with either Zenker's or sublimate. These changes in the color picture were rather more interesting than disconcerting, as the differentiation between the various elements was even more marked when Mallory's stain was used after Beauchamp's fluid than after the commonly used Zenker's.[1]

GENERAL COMPARATIVE DISCUSSION OF THE THREE SPECIES.

External Features.

Phaenocora virginiana, n. sp.: Length of fully extended sexually mature animals 0.7—1.3 mm. It is therefore one of the smallest of the phaenocoras,

[1] Because of the differences in the staining reactions of a given stain under differences in fixation, I have avoided the use of the commonly used expressions, *cynophil* and *erythrophil* which, at best, are very inaccurate and misleading.

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sharing this distinction with *Ph. beauchampi* (0.6—1.2 mm.) and *Ph. achaeorum* (about 1 mm.), although it is impossible to make an exact comparison of the lengths of the various species as each author seems to measure his species in the condition of extension or contraction which is in accord with his idea of what the typical form of his species is. Anyone who has studied rhabdocoeles in general and *Phaenocora* in particular must be aware of the fact that these animals are continually changing not only their length but their shape as well. It would seem advisable, therefore, to endeavor to compare the size and shape of these animals in a condition which will be constant in all species. This condition is assumed by the animal when swimming freely in the fully extended condition. HOFSTEN (1911) among other authors has made use of this condition both in his drawings of the living animal and the measurement of the same; others have used the "freely-crawling condition"; while still others make no mention at all of the condition the animal was in when the drawings or measurements were made. I found that the animals could easily be made to assume the freely-swimming condition by putting them on a glass slide in a thin film of water. They then could be studied satisfactorily under a binocular dissecting microscope and sketches made and measurements taken. *Ph. virginiana* is about $^1/_5$ as broad as long when in the above condition. Fig. 2 (A, B, C, D) shows some of the changes in shape of this animal while under observation for about 15 minutes. The figure on the left (A) shows this animal when fully extended. NASONOV's (1919) drawing of *Ph. achaeorum* (Plate IV, fig. 1) corresponds, for instance, quite well with my sketch (fig. 2, C) of *Ph. virginiana,* while fig. 2, D is reminiscent in no slight degree of FUHRMANN's (1894) and GRAFF's (1904—1908) sketches of *Ph. stagnalis* (*Ph. clavigera*). Possibly the only truly satisfactory method of describing the size and shape of these animals is by the means of photographs, photographed to scale, as the slightest deviation of a line in a sketch from its proper position may lead to an entirely uncharacteristic picture of the animal in question.

While *Phaenocora virginiana* is small in size, it is decidedly robust in its appearance (see fig. 1). The pharynx is relatively large and broad; the body broadens out considerably in its posterior third and tapers out rather suddenly into a relatively long but blunt tail papilla. In front of the pharynx, about half way between its anterior end and the extreme anterior end of the body, are situated normally a pair of reddish appearing eyes. The anterior end of the body in the neighborhood of the pharynx is often heavily pigmented by a granular pigment, which probably corresponds to the "sogenannten Crystaloiden" of GRAFF's (1911) description of *Ph. agassizi,* but while actually rather brownish in color appears rather black in masses. Close inspection shows no difference in the appearance of this pigment and that of the eyes themselves. SEKERA (1904) found the same resemblance between the eye and

body pigment of *Ph. rufodorsata*. Very frequently masses of this pigment are found at the anterior end of the pharynx, and quite typically a ring of the same surround its base (see figs. 1, 4, 5, pg_1). At times, I have observed scattered flecks of pigment along the dorsal side of the body almost to its extreme posterior end. This pigment is very variable including that of the eyes (also see figs. 1, 3, 4, 5). As a matter of fact what appear to be one-eyed individuals are not uncommon. I have before me a total mount of an example of *Ph. highlandense* in which there is no eye-pigment present and the closest observation fails to reveal the slightest trace of any visual apparatus. In this respect this individual belongs to the "blinde Arten" in spite of the fact that in every other respect it resembles a species which possesses eyes. A phaenocora has been observed in which the eye pigment was decreasing in amount from day to day, but the specimen was unfortunately killed while under observation before it could be actually determined whether it would eventually lose all of the pigment. KENK (1925, p. 24) in describing the eyes of *Polycladodes alba,* states that according to his observations they vary in number between 4 and 46 at each side. This variation he ascribed to a periodic degeneration of the eye pigment, as he found fragments of this pigment in the mesenchyme and in the epithelial cells of the gut. He finally says: "Offenbar handelt es sich um eine periodische Degeneration des Pigments, das dann (passiv) gegen den Darm wandert und schliesslich durch diesen nach aussen abgeschieden wird." It would seem that something of this sort must happen in *Phaenocora,* not only with reference to the eye pigment proper but to the body pigment also. SEKERA (1904, p. 441) states that he not infrequently found examples among a large culture of *Ph. unipunctata* which resembled the rest of the individuals of the culture in all respects except that they were blind. In comparison to the above he found among his sketches a drawing of an individual with a broadened hind body after the type of *Derostoma anophthalmum* (= *Ph. vejdovskýi*) which possessed eyes. The first of the above observations is easily explained in the light of KENK's study of the eyes of *Polycladodes alba.* The latter, however, in which a normally "blind" individual possessed eyes is not so easily accounted for unless we go under the supposition that all phaenocoras potentially have the ability to possess eyes or more properly eye pigment. HOFSTEN (1911, p. 40) in speaking of *Ph. clavigera* said that this animal possesses two kinds of pigment—a yellow-red and a more red. The latter he found collected together in longish spots or stripes, and then states further that this pigment is, however, entirely diffuse and eyes can not be spoken of, although naturally a sharp boundary is not present between such pigment and "diffuse eyes". The important thing to my mind, however, is not the question of "diffuse pigment", "diffuse eyes", or concentrated eyes (if we may speak of well marked eyes as such) but whether a visual apparatus is actually present. The

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mere aggregation of a mass of pigment may mean nothing at all from the visual standpoint, such as for instance, the pseudo-eyes of certain lepidopterous larvae. However, HOFSTEN (1918) himself described an actual visual apparatus for *Ph. unipunctata* which is commonly described as having "diffuse eyes". While up to the present time I have made no serious attempt to study the visual apparati of my forms, I am, however, in a position to state that the eye of *Ph. virginiana* differs greatly from the eye of *Ph. unipunctata* as described by HOFSTEN. As a matter of fact, it appears to resemble more closely the eyes of *Mesostomum lingua* and *Mes. ehrenbergii* as described and pictured by LUTHER (1904, p. 80 and Taf. III, fig. 24, 25). In my other two species the visual apparatus seems to differ considerably from either of the above, although I have as yet not worked out the details of the same. The question now resolves itself into this: Are there actually any blind phaenocoras? SEKERA (1904) and others have remarked on the extreme light-shunning habits of the blind phaenocoras. Is this not what one would expect of animals which possess a visual apparatus without pigment? May not after all the so-called "blinde Arten" represent forms in which the pigment of the visual organs is wanting?

Ph. virginiana is typically colored a dark green by the presence of numerous zoochlorellae, which makes the study of the living animal rather difficult. The colorless epidermis reveals dermal rhabdites as described by GRAFF (1911) for *Ph. agassizi.*[1] At either side of the pharynx, arising at points lateral to its base, can be seen lines of long double-pointed rhabdites ("Stäbchenstrassen" *rs*) which meet in the mid-line immediately between the eyes, and from there spread out in a fan-like manner to the "snout" of the animal where they open partly terminally and partly ventrally. Serial sections reveal that these elongated rhabdites take their origin from specialized cells lateral to the base of the pharynx. Each of these cells are capable of producing clumps or rather sheaves of these rhabdites at one time. It has been observed that these rhabdites, which eventually reach the surface in the epithelium of the "snout", are often used by the animal to capture their prey through their adhesive properties.

The genital pore (fig 1, *gp.*) opens on the ventral surface in the mid line at a point some distance in front of the first half of the body. If one be fortunate enough to observe a form not too deeply colored by zoochlorellae, the outlines of the male copulatory organ (*co*), female genital canal (*fgc*), which has a characteristic warty appearance in this species, ovary (*ov*),

[1] The rhabdites of *Ph. virginiana* differ from those of *Stenostomum grandi*, as described by CARTER (1933), in that they do not react to vital staining with Bismarck brown. Furthermore, while they are extremely evident in the living animal and float freely, from the disintegrating epithelium of an animal subjected to pressure, I have been unable to locate them definitely in sections, as they appear to be discharged by any fixing-fluid that I have used. However, the cavities which they have occupied are very evident in transverse sections of the epithelial cells.

and the small and simple bursa intestinalis (*bi*) may be observed. The yolk glands (*yg*) have the net-like structure characteristic of many species of this genus and extend from the region of the genital pore to almost the end of the body. Sometimes the anastomosis of these originally paired structures is not complete and the paired condition is still evident through the swollen condition of the main channels (see fig. 1). In one case it was revealed in sections that these channels had become confluent in the region of the genital pore (see fig. 40, *yg*) and had become swollen to such an extent that they had usurped most of the space between the genital atrium and the enteron. With few exceptions, anteriorly directed extensions of the yolk glands are produced on both sides, up to and often slightly anterior to the base of the pharynx. These extensions are not shown in Fig. 1 but can be seen in Figs. 4 and 5, *yg*. In most cases the ramifications of the yolk glands can be easily followed in the living animal under relatively low power by the use of obliquely directed light. Under these conditions they appear milk-white against a green background. Under higher magnification and direct lighting the yellow droplets of the shell-substance (*ss*) are extremely evident. Under favorable conditions the lateral extensions of the testes (*te*) can be seen from the ventral side lying at either side of the enteron. They are paired, somewhat lobed structures situated at the sides of the dorsal part of the body and extending from the posterior border of the pharynx to about the last third of the body length. Their position, extent, and appearance seems to be quite constant in this species, but the reliability of a description of the testes as a systematic character must always be accepted with caution, as the extent and appearance of these organs are bound to vary with the degree of sexual activity exhibited by the animal at the time of observation. LUTHER (1921, p. 17) remarks with reference to the testes of *Ph. typhlops:* "Die Hoden (Textf. 6 T) sind jederseits etwas hinter der Mitte des Körpers, am lateralen Rand desselben gelegen. Sie sind bald ungelappt, bald gelappt oder in einige getrennte Follikel zerlegt und befinden sich lateral von benachbarten Lappen der Dotterstöcke z. T. aber auch etwas dorsal oder ventral denselben." He then remarks in a footnote (bottom pp. 17 and 18): "Graff (Bronn p. 2527) giebt in der Gattungsdiagnose von *Phaenocora* an, dass die 'Hoden ungelappt' sind. Wahrscheinlich hängt die Lappung zum Teil von dem Entwicklungszustand dieser Organe ab. Bei einem *Phaenocora*-Exemplar mit bestacheltem Penis aus Altrip in der Bayrischen Pfalz, das wahrscheinlich zu dieser Art gehört (eine sichere Bestimmung ist an dem konservierten Tier nicht möglich) finde ich dorsal sehr stark entfaltete, gelappte Hoden, während die Dotterstöcke verhältnismässig klein sind. Vielleicht handelt es sich um sukzessiven Hermaphroditismus? Auch Hofsten (1911) findet bei *Ph. rufodorsata* (p. 35) und *clavigera* (p. 42) stark gelappte Hoden." GRAFF's "Gattungsdiagnose" of the testes of *Phaenocora* seems to be equally inapplicable

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to the testes of my species as, while the testes of *virginiana* are typically slightly lobed, those of *kepneri* are follicular and greater in extent while finally the testes of *highlandense* ramify in an even more complicated manner than those described by BEKLEMISCHEV (1929) for *Phaenocora* (*Megalo-derostoma*) *polycirra*.

I have not worked out the configuration of the excretory system in this form, but the excretory pores open on the ventral surface between the third and fourth fifth of the body length as described by LUTHER (1921) for *Ph. typhlops*.

Phaenocora kepneri n. sp.: Length of fully extended sexually mature animals 2—2.5 mm. It therefore is considerably larger than *Ph. virginiana* and slightly larger than *Ph. agassizi*, which GRAFF (1911) described as being 1.5—2 mm. in length. In the fully extended condition it gives the impression of being much slimmer in outline than the before-described species. As a matter of fact its width is about $^1/_5$ of the body length as in *virginiana*, but the narrower, elongated pharynx and the tapering outline of the anterior end gives the impression of greater slimness. The outline of the posterior end of the body is much more blunt than in the foregoing form, and the tail papilla is much shorter and sharper. While the amount of pigment associated with the eyes together with their pattern varies considerably (see figs. 7 and 8), the anterior end with the exception of the eye spots themselves in all animals so far observed is entirely of almost entirely devoid of pigment. As in the preceding form, apparently one-eyed individuals are not infrequently met with.

Ph. kepneri typically possesses zoochlorellae but seldom in as great numbers as in *virginiana*. As in *Ph. virginiana* dermal rhabdites are present and the "Stäbchenstrassen" conform in general to the condition in the preceding species. Not only are there less zoochlorellae but the body itself seems much more transparent than in *virginiana* or *highlandense*. Because of this, the reproductive organs can be much more easily observed than in either of the other species.

The genital pore (fig. 6, *gp*) lies slightly more anterior than in *virginiana*. The male copulatory organ (*co*) is relatively enormous and the extremely long, S-shaped ductus ejaculatorius (*de*) can be easily recognized together with the "vesicula seminalis" and "granulorum", which are separated from the part in which the ductus ejaculatorius lies by a muscular diaphragm. The thornlets (*t*) may be seen lying in a group at its inner end. Attached to the superior genital atrium may be seen the exterior portions of the pear-shaped appendages (*psa*) of the same which are so characteristic of the genus *Phaenocora*. The female genital canal (*fgc*) is very long and tapers gradually from the superior genital atrium to the point where it meets the short stalk of the bursa intestinalis (*bi*). At this point may be seen 5 extremely large, spherical cells (gc_1) which group themselves about the opening between the

stalk of the bursa and the female genital canal. At this same level the ovary (*ov*) is attached to the female genital canal by means of a very short oviduct. Slightly distal from this point may be seen the "shell glands" (not shown in fig. 6). Under certain conditions it is possible to see the paired yolk ducts that unite to form a short common yolk duct which is seen to empty into the female genital canal at the same point as the oviduct. (The actual morphologigal relationship between these ducts and the oviduct will be discussed in the proper place.) The bursa intestinalis (*bi*) is variable in size and appearance and possesses a short stalk. The exterior is not smooth under ordinary conditions but is elevated into little knobs. Usually, the main cavity of the bursa is surrounded by locules and the whole may be constricted in several places. Frequently the bursa contains living sperms or yolk material and sometimes both. The whole appearance of the female genital canal and its associated organs suggests a swan's neck. This appearance is accentuated by the movements of the animal. At times the bursa may be drawn forward so much that it lies laterally to the posterior end of the pharynx. Sections reveal that this flexibility is made possible by an extremely long ductus bursa-intestinalis. The yolk glands appear to be of a somewhat finer texture than in *virginiana*. Most frequently their anastomosis is so complete that all trace of their original paired condition has been lost. Forward extensions of these glands do not appear to exist as such, but in some cases small yolk glands lie anteriorly one at each side of the posterior half of the pharynx which appear to have no direct connection with the yolk glands proper. The testes (*te*) present a folicular structure and vary in size with the condition of the animal. In some cases they almost meet in the mid dorsal line, while in others they are confined to the lateral borders of the body. The testes have a much greater extent than in *virginiana*, extending from just behind the pharynx to the posterior end of the enteron. As in the preceding species, I have not worked out the configuration of the excretory system but the position of the excretory pores and the main stems of the proto-nephridia are as described for *virginiana*.

Phaenocora highlandense, n. sp.: Length of fully extended sexually mature animals 3—3.7 mm. It is therefore the largest of my three new species. It is not only larger than the preceding form but it is sturdier in its appearance. The anterior end of the body is broader and pharynx thicker than in *virginiana*. The posterior end of the body is usually broad and the tail papilla is short and blunt (see fig. 9). Zoochlorellae are usually present, but when few in number or entirely wanting, the body has a milky or opalescent hue which makes the external study of the internal organs rather difficult. Unlike the condition in the before-described species, the pigmentation of the eyes differs from that of the anterior part of the body. The fore part of the body as far back as the base of the pharynx is colored a deep red by some pigment which is soluble in alcohol, as it does not appear in sections or in total

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mounts of the animals. The pigment of the eyes is granular in texture and seems to be identical with the eye and body pigment of *Ph. virginiana* and *kepneri*. In both respects its pigmentation seems to agree with that of *Ph. clavigera* as described by HOFSTEN (1911, p. 40). The alcohol soluble pigment seems to correspond to the yellowish red pigment of *Ph. clavigera*, while the second seems to agree with the aggregated pigment which was collected into three longish spots or stripes. It is worthy of note that in my "eyed" form, *Ph. highlandense*, the aggregated pigment seems to be confined to the neighborhood of the eyes, while in the "blind" form, *Ph. clavigera*, this pigment is collected into three longish stripes. Is it not possible that eyes may be located in this pigmented area also? It was in an individual of the species *highlandense* that I observed the "blind" condition (cf. pp. 294, 295). The "Stäbchenstrassen" agree in general with those of the two preceding species and in this species a few sparsely scattered, very slender dermal rhabdites are present which are about the height of the thickness of the epithelium.

The genital pore (fig. 9, *gp*) opens in relatively the same position as in *Ph. kepneri*; the inferior genital atrium (*iga*) appears almost spherical in outline and the musculature is quite evident. Partly anterior and dorsal to it may be seen the superior genital atrium (*sga*) and its pear-shaped appendages (*psa*). The pear-shaped copulatory organ (co) is relatively small and the ductus ejaculatorius is rather short and relatively straight and the thornlets (*t*) can be seen aggregated in a group near its inner extremity. The female genital canal (*fgc*) is short and thick. The bursa intestinalis (*bi*) is attached directly to the end of the female genital canal and not by means of a short stalk as in *Ph. kepneri*. There are no typically spheroidal cells arranged about the junction of the female genital canal and the bursa intestinalis as in foregoing species. The ovary (*ov*) is attached to the female genital canal by means of a short oviduct but the point of attachment is not at the point of union between bursa and female genital canal in the other two Virginia species but at a point somewhat distal from it. As in the preceding species, the common yolk duct enters the female genital canal at the same point as the oviduct. Slightly distal to the point of entrance of the oviduct may be seen the shell glands. The testes, not shown in figure, are dorsal in position and extend from slightly behind the pharynx nearly to the posterior end of the enteron. They ramify very intricately and are even much more complicated than those described for *Phaenocora* (*Megaloderostoma*) *polycirra* by BEKLEMISCHEV (1929, p. 544 and Abld. 2). Each testis is made up of ramifying tubules which in their entirety resemble a wing. These "wings" meet in the mid-dorsal line but do not anastomose to form a single testis but, on the contrary, each retains its own individuality. The yolk glands (*yg*) of the ventral side are net-like and as far as observed showed no sign of their original paired condition. Furthermore, they extend

anteriorly on either side of the pharynx and bend dorsally, forming above the pharynx dorsal extensions of themselves which extend over the posterior half of the pharynx and posteriorly to it as far back as the anterior extensions of the testes—in some cases even beyond. These paired dorsal extensions of the yolk glands, not shown in figure, do not anastomose to form a single yolk gland but each has a decidedly hand-like structure with widely extended fingers directed toward the mid-dorsal line. These dorsal extensions of the yolk glands are very characteristic of this species and one can not miss observing them even under a most superficial inspection. BRAUN (1884, p. 227 and Taf. 1, Fig. 8) describes quite similar dorsal yolk glands for *Ph. baltica* but states that they do not stand in direct communication with the ventral glands.[1]

In two respects therefore this animal shows very characteristic structures: namely, the possession of dorsal extensions of the yolk glands and the presence of peculiar ramifying testes. The latter characteristic seems to be unique in the genus although the condition is somewhat approached in *Ph.* (*Megaloderostoma*) *polycirra*.

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I have worked out somewhat more of the configuration of the excretory system of this form than in either *virginiana* or *kepneri*. In general it follows rather closely the description of the excretory system of *Ph. stagnalis* Fuhrm. (= *Ph. clavigera* Hofsten) given by FUHRMANN (1894) and GRAFF (1904—1908, p. 2147, 2148 and fig. 30). The position of the open excretory pores (fig. 9, *ep*) and the main stems (*ms*) of the proto-nephridia is approximately as in *virginiana* and *kepneri*. Each main stem forms a loop at its proximal end and extends posteriorly as a posterior branch (*pb*). From the loop of each main stem is given off an anterior branch (*ab*) which extends forward along the side of the pharynx. At about the level of the mouth, each anterior branch is seen to bend abruptly toward the mid-line and then bend outward again for a short distance where it straightens out to run anteriorly again to a point just posterior to the eye, where it bifurcates, forming an outer and inner branch, the latter ending blindly in a tri-lobed pocket. At the point where each branch continues in a straight line after bending back from its position in front of the mouth is given off a branch which runs back posteriorly and lies dorsally to the main anterior branch. The two main anterior branches are connected together in front of the mouth by means of a commisural vessel (*cv*). I was able to observe that a branch vessel from either side takes its origin from flame-cells in the neighborhood of the genital pore but I was unable to locate its connections with the main system. With the exception of the commisural vessel connecting the two anterior branches in

[1] BEKLEMISCHEV (1929, p. 544), in summarizing the characters of *Ph.* (*Megaloderostoma*) *polycirra*, gives four characters which he considers unique in his species. Among these is the possession of independent dorsal yolk glands. He has evidently overlooked BRAUN's description of *Ph. baltica*.

front of the mouth and the straight sections of the same running toward the eyes, the configuration of the main vessels of the excretory system of *Ph. highlandense* agrees very well with FUHRMANN's figure of the excretory system of *Ph. stagnalis*.

MORPHOLOGY OF THE REPRODUCTIVE SYSTEMS OF PHAENOCORA VIRGINIANA, PHAENOCORA KEPNERI, AND PHAENOCORA HIGHLANDENSE.

As I have already mentioned, it is impossible to arrive at a clear conception of the morphological relationships of the various organs of the reproductive system without a combined study of the living animals, total preparations, and serial sections. Diagramatic reconstructions of the reproductive systems of my three species are shown in textfigure 1, A, E, B. A comparison of these reconstructions with figs. 1, 6, and 9 of the living animals, together with fig. 41, a camera lucida drawing from a total mount of *Ph. virginiana* in which happily the organs show little or no distortion of their living condition, will serve to clarify the discussion to follow.

The genital pore (*gp*) leads directly into the atrium inferius (*iga*) which is lined by a ciliated epithelium made up of cells very similar to those which clothe the exterior of the body. The atrium inferius is separated from the roomy atrium superius (*sga*) by a constriction, the size of the lumen of which is controlled by circular muscles. The extent of the cavity of the atrium inferius is ordinarily much greater in the living animals than in sections. The inferior atrium does not lie directly ventrally to the superior atrium but slightly posteriorly and ventrally to it. In reconstructions, based upon sections, of the species of many authors, the atrium inferius is shown as lying absolutely ventrally to the atrium superius. This position may, of course, be peculiar to their species, but I am inclined to think that they have a false idea of its position due to putting too much emphasis on the study of serial sections in which distortion has occurred. In fig. 51, a drawing of a section through the copulatory organ and genital atria of *Ph. kepneri*, it will be seen that the atrium inferius (*iga*) lies in almost its true relationship to the atrium superius while, as will be explained later, the copulatory organ has been forced out of its natural position through shrinkage due to fixation. On the contrary in fig. 50, drawn from another series of sections of the same species, the atrium inferius (*iga*) is not only pulled out of its normal position but is greatly stretched as well. In fig. 16, the atrium inferius not only lies immediately ventral to the atrium superius but it is furthermore distorted through the intrusion of the partially evaginated end of the copulatory organ.

The male copulatory organ opens into the atrium superius slightly to the left of the mid-line. Its longitudinal axis is not parallel to the longitudinal axis of the body, but forms an acute angle with it (see figs 1, 6, 9, and 41). Furthermore, its longitudinal axis is normally nearly parallel to the ventral surface of the body as in fig. 50 and not as in fig. 51, in which the contraction of the anterior part of the body through fixation has pushed the pharynx back against the copulatory organ so that the longitudinal axis of the copulatory organ forms an angle of 45° or more with the plane of the ventral surface of the animal posterior to the genital pore. I have before me two schematic reconstructions of *Ph. unipunctata,* the first by LIPPITSCH (1890, p. 156) and the second by BENDL (1909, fig. 2, p. 298). In the first case, the position of the atrium inferius and the copulatory organ seems to be entirely erroneous, especially the copulatory organ which is shown in an almost vertical position. In the second case the male copulatory organ and the atrium inferius are drawn in practically their normal position. LIPPITSCH's reconstruction was, according to him, made entirely from serial sections. BENDL does not state from what sort of data his reconstruction was drawn.

Attached to, and actually forming an integral part of, the atrium superius are the so-called "pear-shaped lobes" (see fig. 41, *psa*) which will be discussed at length in the proper place.

The female genital canal enters the atrium superius slightly to the right of the mid-line very close to the distal end of the copulatory organ and slightly dorsally to it. It varies greatly both as to its length and appearance in my three species (see text-fig. 1, A, E, B, and fig. 41). At its proximal end is found the bursa-intestinalis, which in turn communicate with the enteron—by a simple pore in *Ph. virginiana,* and by a duct in *Ph. kepneri* and *Ph. highlandense.* The nature of this communication between the female reproductive organs and the enteron will be discussed below:

The "Geschlechtstrakt-Darmverbindung".

BENDL (1909, p. 294—299 and text-fig. 2) described the presence of a communication between the female reproductive organs and the enteron, "ductus genito-intestinalis", in *Ph. unipunctata.* Since then such a mode of communication has been described in some detail by COGNETTI DE MARTIIS (1916) for *Ph. jucunda* and by LUTHER (1921) for *Ph. typhlops* and *typhlops*

Text-figure 1. Diagramatic reconstructions of the reproductive organs of several phaenocorans.

A. *Phaenocora virginia* n. s.
B. *Phaenocora highlandense* n. sp.
C. *Phaenocora unipunctata* Örsted, 1843.
D. *Phaenocora megalops* Duges, 1830.
E. *Phaenocora kepneri* n. sp.
F. *Phaenocora (Megalodcrostoma) polycirra* Beklemischev, 1929.

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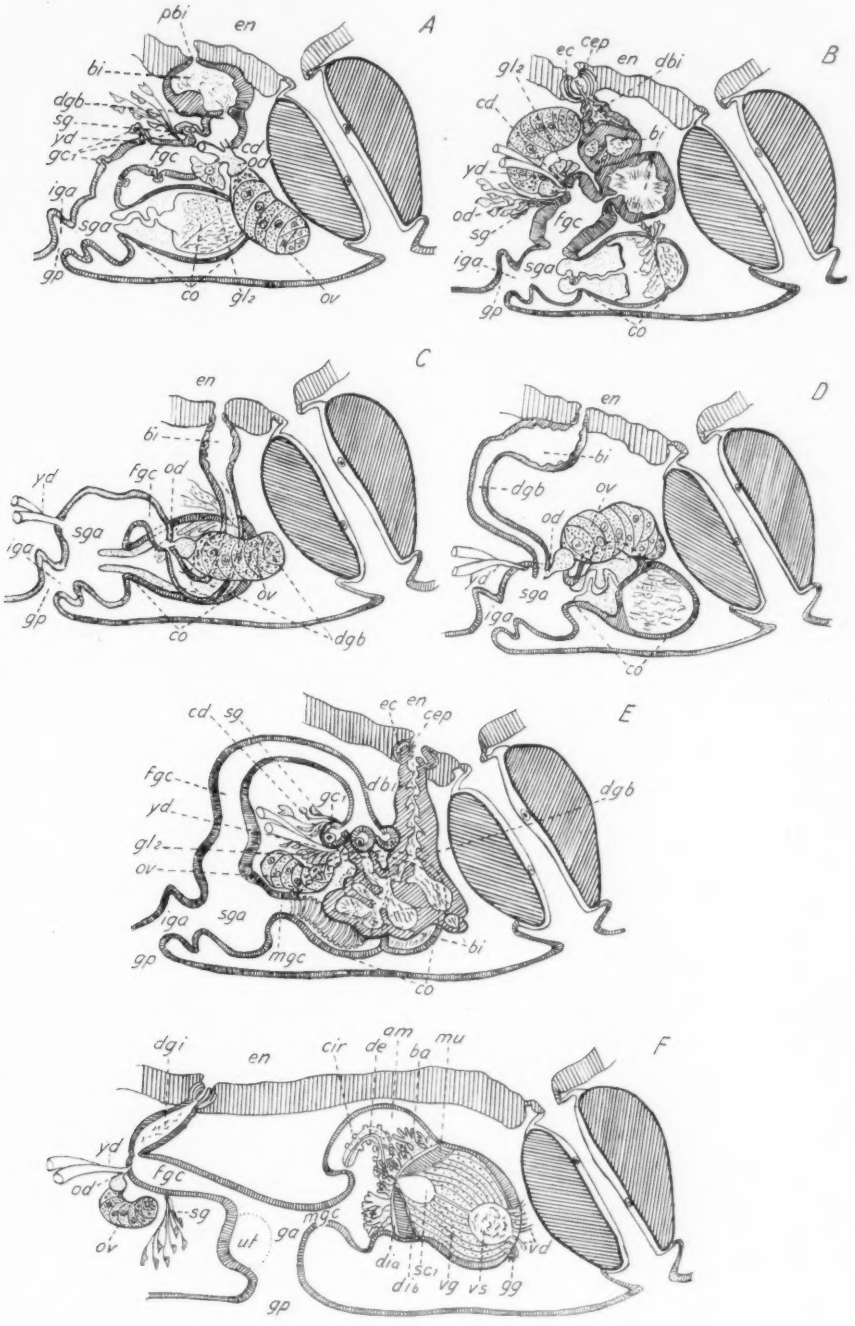

Text-figure 1.

subsalina. It has furthermore been mentioned by BEKLEMISCHEV (1929) as occuring in *Ph.* (*Megaloderostoma*) *polycirra* and by MEIXNER (1915) as probably occuring in *Ph. variodentata*. This communication between the female genital organs and enteron is present in all of my three species, though varying in detail, and is in all probability present in all phaenocoras.

I have no intention of reviewing all the literature relative to the occurence of this connection between the female genital tract and the enteron in the flatworms, but in order to discuss intelligently the morphological differences exhibited in the details of this communication among my three species of *Phaenocora*, as well as in the other known species of this genus, it will be necessary to consider the probable phylogenetic origin of this communication and its further differentiation among the more advanced forms.

STEINBÖCK (1924) advanced the theory that primitively the egg of the Platodes passed into the middle parenchyma and from thence through the mouth-opening to the exterior as is still the case among the present-day Acoela. REISINGER (1929) added considerably to this theory by his observations relative to his *Bresslauilla relicta*, *Oekiocolax plagiostomorum*, etc. Briefly the theory in its present-day condition may be outlined as follows:

1. In *Acoela* the egg enters the middle parenchyma and passes to the exterior through the mouth-opening.
2. In the *Catenulidae* (Rhabdocoela) and in *Hofstenia* (Alloeocoela) the egg passes into the enteron by a rupture of its wall and from thence to the exterior through the mouth-opening.[1]
3. In *Bresslauilla relicta*, Reisinger (Rhabdocoela, *Graffillidae*) the egg passes into the enteron through a "communicatio genito-intestinalis" and from thence by way of the mouth-opening to the exterior.
4. Among the Alloecoela, in the *Prorhynchidae* and in *Bothrioplana*, a duct (ductus genito-intestinalis) connects the atrium feminum with the enteron, but no longer functions as a duct for the passage of the egg which is carried to the exterior by a female genital pore.
5. In *Coelogynopora bresslaui*, Steinböck (Alloeocoela) the egg passes to the exterior by means of a female genital canal, atrium, and genital pore. In this species the female genital canal is connected with the enteron by means of a "ductus genito-bursalis" communicating with the "bursa intestinalis" and the latter with the enteron by a "porus bursa-intestinalis".

[1] It has been observed in this laboratory that at least some species of the Catenulidae do not normally lay their eggs by way of the enteron and mouth-opening. Observations on stenostoma, which were sexually mature as females, showed that their eggs passed to the exterior by means of temporary openings in the mid-line of the ventral side of the body. On one occasion only was it found that an egg entered the enteron and finally passed to the exterior by means of the mouth-opening and, incidentally, this egg failed to develop.

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6. In some phaenocora and in some species of other genera, the bursa-intestinalis has become separated from the enteron but still communicates with it by means of a "ductus bursa-intestinalis".
7. Finally, in many forms the ductus bursa-intestinalis completely disappears and the bursa-intestinalis becomes entirely freed from any means of communication with the enteron.[1]

STEINBÖCK (1924, pp. 472—475) discusses in some length the physiological and morphological considerations concerned with an attempt to arrive at a satisfactory nomenclature for the description of all conditions which may arise from the differentiation of the primitive "Geschlechtstrakt-Darmverbindung". He finally summarizes his efforts as follows (pp. 473—474):

"Es wird daher zweckmässiger sein, bei Tieren, die eine Verbindung des Geschlechtsapparates mit dem Darm besitzen, vorerst ganz allgemein von einer *Geschlechtstrakt-Darmverbindung, Communicatio genito-intestinalis* zu sprechen und dann erst im besonderen zu untersuchen, um was für eine Verbindung es sich handelt. Ist es lediglich ein einfacher Gang zwischen dem Geschlechtsapparat und dem Darm, so bezeichnet man ihn auch weiter hin als Ductus genito-intestinalis. Ist jedoch eine Bursa intestinalis vorhanden, dann wird man Namen anzuwenden haben, die das morphologische Verhältnis klar ausdrücken. So schlage ich für jenen Gang, der von seiner Vereinigungsstelle mit den Oviducten bis zur Einmündung in die Bursa reicht, den Namen *Ductus genito-bursalis* vor, zu deutsch etwa Bursastiel, um einem von den Tricladen her bekannten Ausdruck anzuwenden und für einen zwischen Bursa und Darm etwa auftretenden Gang *Ductus bursa-intestinalis*. Besteht überhaupt keine Gang, so ist eben nur eine Communicatio genito-intestinalis vorhanden, die durch die Bursa intestinalis vermittelt wird, falls sich diese Darm abgesackt hat."

If we accept STEINBÖCK's interpretations as stated above we must consider the extent of the communicatio genito-intestinalis, in all forms that possess a bursa intestinalis, as reaching from the point of its union with the oviduct to its point of entrance into the enteron.

In *Ph. virginiana* (see figs. 10, 17, 18, 22, and 24) the bursa intestinalis is a relatively simple structure, the cavity of which opens directly into the enteron without the intervention of a ductus bursa intestinalis. It may therefore be considered as possessing a porus bursa intestinalis (*pbi*). In this respect it may be said to resemble the condition represented in *Coelogynopora* but, on further observation, it will be seen that histologically its cells differ greatly from those of the epithelium of the gut. By comparing my figures (figs. 22 and 24) of the bursa intestinalis of *Ph. virginiana* with that of STEINBÖCK's (1924, Abb. 7, p. 468) figure of the bursa and porus of *Coelogynopora*

[1] For the sake of brevity I have omitted all mention of the condition of the "Geschlechtstrakt-Darmverbindung" in the triclads, polyclads and monogenetic trematodes. For those interested in this subject I can recommend the excellent papers of Bendel, Steinböck, Bock, Reisinger, Meixner, and others and Bresslau's general discussion in the *Handbuch der Zoologie*. (Kükenthal and Krumbach.)

bresslaui, it will be seen that while the transition between the epithelium of the enteron and that of the bursa intestinalis is very evident in his form, nothing of the sort takes place in *Ph. virginiana*. Furthermore, in *C. bresslaui* the boundary of the porus bursa-intestinalis is produced by a simple folding-over of the transitional cells of the epithelium of the enteron and there does not seem to be present any mechanism for reducing or closing the porus. In *Ph. virginiana*, on the other hand, (see figs. 22 and 24) the porus bursa-intestinalis is guarded by a rather complicated valvular apparatus in which the cells have a decidedly petal-like arrangement. In figs. 22 and 24 this valve-like structure (*vc*) is open, and sperms can be seen being discharged into the enteron. Whether this valve-like structure ever becomes so widely expanded in the living animal is a matter of conjecture, but, not infrequently, living sperms have been seen swimming freely in the enteron, although it is possible that this was due to pressure exerted by the cover-glass. The cells which make up the wall of the bursa intestinalis vary greatly in size and shape (see fig. 17, a horizontal section through the bursa very close to the porus, as well as the previously-mentioned figures). Especially when fixed with BEAUCHAMP's fluid, they have a characteristically plump appearance. The nuclei are large and possess a single nucleolus and peripheral chromatin. The cytoplasm seems to be finely granular and not fibrillar as described by COGNETTI (1916, p. 229) for *Ph. jucunda*. The cavity of the bursa intestinalis is simple and possesses no intra-cellular lumina and complicated extensions of its cavity (the "Nebenhohlräume" of STEINBÖCK) as described for *C. bresslaui*, which are also extremely evident in the bursas of *Ph. kepneri* and *Ph. highlandense*.

In *Ph. virginiana* the oviduct opens into the proximal end of the female genital canal (see fig. 41, *od*). If we are to accept STEINBÖCK's definitions as outlined above, the *ductus genito-bursalis* should extend from the mouth of the oviduct to the bursa intestinalis. In *Ph. virginiana* the structure which corresponds morphologically to the ductus genito-bursalis of STEINBÖCK has very little resemblance to a duct as such, but is an almost conically shaped structure forming a valve-like arrangement which serves to shut off the bursa intestinalis from the female genital canal (see fig. 41 and text-fig. 1, A, *dgb*).

In *Ph. kepneri* the "Geschlechtstrakt-Darmverbindung" forms a very much complicated apparatus than in *Ph. virginiana* (see figs. 14, 15, 19, 20, 21, 23, and text-fig. 1, E). In this species the bursa has retreated a considerable distance away from the enteron (see text-fig. 1, E and figs. 14 and 15), which latter were drawn from the same series of section, which has resulted in an interpolation of a *ductus bursa-intestinalis* between bursa and enteron (*dbi*). The bursa intestinalis, instead of being small and simple as in *Ph. virginiana*, is usually very large and thrown into numerous folds and prominences by means of the constrictions of many irregularly arranged muscle

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fibers (see fig. 19, *mf*).[1] VEJDOVSKY (1895, p. 119) states that the empty spermatheca (= bursa intestinalis) is an externally contracted and inwardly a very shrivelled organ, which last property is due to the strong, separate cuticular endowment of the inner lumen. I, however, have never been able to demonstrate a cuticular lining of the bursa intestinalis of any of my three species and I feel that the folded or shrivelled appearance of the bursa is due to the constrictions formed by the contracted muscle fibers. Furthermore, this shrivelled appearance is not confined by any means to the *empty* bursa, for by referring to my figures, it will be seen that the "shrivelled" bursa is almost filled with sperms. The cells which compose the ductus genito-intestinalis, the bursa intestinalis, and the ductus bursa-intestinalis are very characteristic but rather difficult to describe. These cells are very large and possess irregular plasma-like processes which may be extended into the lumen of the organ. This condition is especially noticeable in the structure of the ductus bursa-intestinalis (see figs. 14, 20, 21, 23) whose lumen is very irregular in outline due to the intrusion of these plasma-like processes. By observing fig. 14 it will be seen that the ductus bursa-intestinalis is a chimney-like structure whose wall is composed of the overlapping processes of the before-mentioned cells. COGNETTI DE MARTIIS (1916, p. 230) considers that the lumen of the receptaculum seminis (= bursa intestinalis), its duct (female genital canal), and the first part of the ductus genito-intestinalis (= ductus bursa-intestinalis) of *Ph. jucunda* to be of an intra-cellular nature. I admit that cell-limits are somewhat hard to define in all cases in these structures in *Ph. kepneri* and that nuclei are not very numerous; still I feel certain that the main cavity of the bursa and its ducts are lined with an epithelium which in many places is hard to demonstrate because of the before-mentioned cytoplasmic processes. There are, however, many side extensions of the main cavity that are undoubtedly of intracellular nature (see figs. 15, 19, 20, *icc*) which in all probability correspond to the "Nebenhohlräume" of the bursa of *Coelogmopora* as mentioned by STEINBÖCK. COGNETTI (1916, pp. 229, 230) states that the cells forming the lining of the ductus communis (female genital canal), receptaculum seminis (bursa intestinalis), and ductus genito-intestinalis (ductus bursa-intestinalis) have bases that are made up of fibrils which

[1] Since making the above observations, I have sectioned an individual of *Ph. virginiana* in which the bursa intestinalis, though small, was very much folded and shrivelled. It contained no sperm but the dorsal portion contained yolk material. The yolk glands were very much swollen and an egg was being formed in the superior atrium. The egg shell was not completely formed and shell forming material was exuding from the female genital canal in the form of a thick thread. The testes were very small and no sperm were found in the vasa deferentia or the vesicula seminalis. This condition is very unusual as these animals are usually sexually mature as males and females at the same time. This illustration serves to show how unreliable as systematic features organs are that are subject to physiological variations and how careful one must be in making descriptions from insufficient material. Incidentally, this was the twenty-sixth slide I had studied of this species and it is the only one in which I found this condition to obtain.

extend toward their free surfaces in a rectilinear manner, and that between these fibrils is a granular cytoplasm which extends outward to form a granular layer which is capable of being raised into lobes. He furthermore states that the fibrillar layer is most pronounced in the receptaculum (bursa) where the granular layer is less evident, and that the granular layer is most pronounced in the ductus genito-intestinalis (= ductus bursa-intestinalis) and ductus communis (= female genital canal). As has already been stated, he considers the lumen of these organs to be intracellular and he states that transverse sections show a very great structural analogy to the so-called "tube à bâtonnets" of Prenant, Bouin Millard, or the "Stäbchenepithel" of Heidenhain, and concludes that they have a similar functional analogy and are, therefore, of a secretory nature. I can, at least in part, confirm the findings of COGNETTI in the structure of these cells in *Ph. kepneri.* I have, however, but seldom been able to demonstrate the fibrillar nature of the cells of the bursa and never all of the cells at one time. That is, one or more cells might show this fibrillar structure of the base, while the others would show no trace of the fibrils. In most cases none of the cells would show this structure and in no case did I find any of these basal fibrils in the cells that compose the ductus bursa-intestinalis, as shown in COGNETTI's fig. 27 (see my figs. 14, 15, 20, 21, and 23). I found, however, that this fibrillar structure of the base of the cells that compose the epithelium of the female genital canal to be very strongly marked in all my species, and even persists after all other structural features of the epithelium have degenerated even to the loss of their nuclei, as will be explained later in the proper place. I am not able to explain why these fibrils should be present in some of the cells of the bursa and absent in others or even may at times be entirely wanting. I can only suggest that it may be due to the physiological condition of the cells themselves at the particular time of fixation. One might consider it a matter of fixation but it would hardly seem probable that several cells out of the whole bursa would be properly fixed so as to demonstrate these structures, while the rest would not.

Figs. 21 and 23 show that the cells (*ec*) which make up the external layer of the valvular apparatus which guards the lumen of the ductus bursa-intestinalis have unquestionably been derived from the epithelium of the enteron. In this respect the valvular apparatus appears to be more primitive than in *Ph. virginiana* where there seems to be no well-defined transitional cells. LUTHER (1921, p. 25), in speaking of the ductus genito-intestinalis (= ductus bursa-intestinalis) of *Ph. typhlops,* says: "... Im Inneren des Duct. genito-intestinalis fand ich meist Zerfall begriffene Dottermasse, an den gelben Dottertröpfchen (Schalensubstanze) leicht erkennbar, und diese Masse liess sich in mehreren Fällen bis in den Darm verfolgen. Spermien habe ich nie mit Sicherheit in dem Gang gefunden, was ich als einen Zufall betrachte

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(vgl. Vejdovský 1895, p. 119)." In my sections, on the contrary, I have in most cases found sperms in great quantities in the ductus bursa-intestinalis and only very rarely yolk or yellow shell material. Fig. 21 shows great masses of sperms being discharged into the enteron. The circular muscle fibers (*cmf*) which usually constrict the lumen of the duct and especially guard the mouth of the valvular apparatus, have evidently become very much relaxed in the process of killing and fixing, resulting in the discharge of a large number of sperms before fixation had become complete. Fig. 23 exhibits a more normal picture with only a small number of sperms being discharged into the enteron and the lumen of the duct very nearly occluded by the cytoplasmic end-processes of the cells which compose its walls. The question now arises: Are living sperms normally ever discharged into the enteron, or only yolk, shell material, and disintegrating sperm? If one will carefully examine fig. 20, it will be seen that many of the epithelial cells of the enteron contain sperms in vacuoles (*sp*). It seems quite evident from this fact that living sperms must have been discharged into the enteron and taken up by its epithelial cells before the animal had been killed and fixation had started. On page 44, I made the statement that living sperms had, not infrequently, been observed swimming freely in the enteron of the living phaenocora, but pointed out that this condition might not be normal, as it was possible that it might be due to the pressure exerted by the cover-glass. The evidence exhibited by the series of sections of which fig. 20 is a sample, however, seems to conclusively establish as a fact that the living sperms are normally discharged into the enteron. It also appears that the enzymes of the gut do not readily kill the sperms and that their digestion is effected in an intracellular manner by the epithelial cells of the enteron.

The ductus genito-bursalis (fig. 15 and text-fig. 1, E, *dgb*) is nothing more than the short stalk of the bursa and is histologically identical with it. It bears little resemblance to the valve-like structure of *Ph. virginiana,* although its lumen is guarded by irregularly arranged ring-muscles.

Vejdovsky (1895, p. 119) states that the spermathaeca (= bursa intestinalis) is divided into two chambers by a constriction and that the chamber into which the stalk empties lies ventrally, while the other lies dorsally, so that in the empty condition it may easily be overlooked. I am by no means sure of what he means by this statement but I am inclined to think that his dorsal chamber might be in part the ductus bursa-intestinalis. In *Ph. highlandense* there is habitually a dorsal and a ventral chamber of the bursa and the ductus bursa-intestinalis communicates directly with the dorsal chamber, in a manner which will be explained in the description of the bursa of that animal. It is difficult to give a satisfactory description of a structure so variable in its appearance as the bursa-intestinalis of *Ph. kepneri.* In general, however, it may be said that the ductus genito-bursalis opens into a relatively

large chamber (see fig. 15). This chamber communicates laterally with a locuolated portion of the bursa (see fig. 14) which is in direct communication with the ductus bursa-intestinalis.

In *Ph. highlandense,* the bursa intestinalis (fig. 16, bi_1, bi_2) resembles more closely VEJDOVSKY's description of that organ than the bursas of either of the preceding forms, in that it is divided into a ventral (bi_1) and a dorsal (bi_2) chamber. These chambers are separated from one another by a well-marked constriction. The dorsal chamber is in direct communication with the ductus bursa-intestinalis, while the dorsal and ventral chambers communicate by means of a rather narrow lumen through the portion of the bursa not completely cut off by the before-mentioned constriction. The walls of the bursa resemble closely the description of the walls of *Ph. jucunda* as described by COGNETTI as no cytoplasmic endprocesses of the cells that compose them extend into its lumen. I have, however, been unable to demonstrate satisfactorily the fibrilar structure of the base of the cells as described for his species. Large intracellular cavities (Nebenhohlräume) (*icc*) are characteristic of the bursa of *Ph. highlandense.*

The ductus bursa-intestinalis, although considerably shorter in length, shows very much the same structure as in *Ph. kepneri.* The valvular apparatus (see figs. 25, 26, 29, 30), guarding its proximal end, resembles somewhat that of *Ph. kepneri* although the number of the sheathing cells (*ec*) is much greater. The longitudinal section (see fig. 29) shows that there are at least four layers of these cells (*ec*) sheathing the cytoplasmic end-processes (*cep*) of the cells which compose the epithelium of the ductus bursa-intestinalis proper, while circular muscles (*cmf*) control the size of its lumen. LUTHER (1921, pp. 23—25, Pl. I, figs. 6, 7, 8, 10, 11, and 12) describes in some detail the receptaculum seminis (= bursa intestinalis) and the ductus genito-intestinalis (= ductus bursa-intestinalis). His fig. 8, a longitudinal section through the valvular apparatus, shows a marked resemblance to my fig. 29. With reference to his figure he says on page 25: "Ein Exemplar aus Heidelberg (fig. 8) weicht insofern ab, als der ganze Apparat plumper erscheint, und die obere Ringfalte weniger scharf ist. Vielleicht handelt es sich bloss um eine postmortale Quellung, da die Epithelzellen des Ductus genito-intestinalis (rechts in der Figur) ebenfalls z. T. gequollen erscheinen." From the above quotation it would appear that LUTHER considers this plump condition of the cells of the ductus bursa-intestinalis to be abnormal. If we examine his figs. 6 and 7, it will be seen that the walls of the bursa intestinalis and to a lesser degree the cells which compose the valvular apparatus are very much shrunken, so much so, in fact, that there is no trace of cell boundaries. In many cases, I have gotten similar results from sublimate fixation which, incidentally, I avoid as much as possible because of this tendency toward the shrinkage of cells. I feel that his fig. 8 represents a condition which is far

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more normal than that which is exhibited in his other drawings. LUTHER's fig. 10 shows a transverse section through the valvular apparatus and the radial arrangement of the cells which compose it. The lumen (L) appears to be quite regular in outline and one would judge by its appearance that it might be lined by a cuticle. Although I have been unable to get a satisfactory transverse section of the valvular apparatus, it will be seen by examining my figures that no such regular lumen is present in my forms, but that the cytoplasmic end-processes of the epithelium of the ductus bursa-intestinalis extend upward between the sheathing cells. His figures 11 and 12 are labeled as representing transverse sections through the valvular apparatus at different levels. This seems hardly possible as there is no indication of the cell-boundaries of the layers of cells which make up the organ. It seems quite probable to me that these figures might be mislabeled and that they may represent transverse sections through the ductus bursa-intestinalis. If one examines these figures, it will be seen that the cytoplasm of the epithelium is homogeneous and that there is no indication of cytoplasmic end-processes. The whole picture, as represented in LUTHER's figs. 11 and 12, would indicate that the lumen was intracellular. In contrast, my fig. 33 represents a nearly transverse section through the base of the ductus bursa-intestinalis of *Ph. highlandense*. The irregular lumen and the cytoplasmic end-processes of the cells are quite evident. Only one nucleus (*nu*) appears in this section. The other structures (*gl*) that superficially might be mistaken for nuclei appear to be of a glandular nature and are filled with a granular secretion. It might be well to mention that the cytoplasmic end-processes of the cells which compose the epithelium of the ductus, always extend proximally, thus helping to prevent any material which may enter the lumen of the ductus from returning to the bursa.

In all the material I have studied, I have been unable to demonstrate a ductus genito-bursalis in *Ph. highlandense*. The bursa intestinalis communicates directly with the female genital canal without the intervention of a ductus (see fig. 16) by means of a narrow lumen which opens into the bursa at the top of a large conically-shaped papilla. It seems impossible to fit this case to the nomenclature set up by STEINBÖCK for the description of these structures, as he defines the limits of the ductus genito-bursalis as extending from the mouth of the oviduct to the bursa itself. If we adhere to his definition in this case, we appear to be in some difficulty. By examining my fig. 16 and text-fig. 1, B, it will be seen that the oviduct enters the female genital canal some little distance from its proximal end. Then, if we adhere to STEINBÖCK's definition, we must assume that the ductus genito-bursalis extends from this point to the bursa. Two serious objections to this interpretation may be put forward: first, there is no indication of the presence of a separate duct as such; second, this region is histologically similar to the

rest of the female genital canal and is enclosed within the muscular tunic which encloses the same. LUTHER (1921) makes no mention of a stalk (ductus genito-bursalis) of the bursa of *Ph. typhlops* nor does he show any such structure in either of his schematic figures (his text-figs. 1 and 7) but, on the contrary, shows the female genital canal as leading directly into the bursa. VEJDOVSKY (1895, p. 118) states that the possession of a short stalk to the spermatheca is a good systematic index of the Derostoma (= Phaenocora) -species. Despite this fig. 39 of *Ph. typhlops* does not show a stalk. However that may be, I have found no stalk to the bursa of *Ph. highlandense* and it would seem that LUTHER has found no such structure in *Ph. typhlops*.

In closing my description of the "Geschlechtstrakt-Darmverbindung" of my forms I may say that these structures are very variable in appearance, due, no doubt, to varying degrees of sexual activity and at best may be used as systematic indices only with extreme caution.

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The Female Genital Canal and its Associated Organs.

The female genital canal extends from the "Geschlechtstrakt-Darmverbindung" to the superior genital atrium (see figs. 10, 11, 12, 14, 15, 16, 31, 41, and text-fig. 1, A, E, B, *fgc*). It may be described as a tube lined potentially by a thick epithelium and enclosed in a muscular tunic consisting of very powerful inner ring-muscles and much weaker and finer longitudinal muscles.

Most authors describe the lining of the female genital canal as consisting of a thick epithelium but COGNETTI (1916, p. 230) considers its lumen to be of an intracellular nature. I must confess that for some time I have been very much mystified as to the nature of the lining of the female genital canal in my forms. In some cases it is lined by a very definite thick columnar epithelium with large basal nuclei. This condition is shown very well in my fig. 34, an almost longitudinal section envolving the end of the female genital canal of *Ph. highlandense*. By examining this figure it will be seen that the cytoplasm of the cells which compose the epithelium is very fibrillar and that there is little or no granular cytoplasm which could be extended into end-processes as in the epithelial cells of the ductus bursa-intestinalis. This fibrillar condition of the cells has already been pointed out by COGNETTI (1916) for *Ph. jucunda* but, as I have mentioned before, he considers the lumen to be intracellular, based on some transverse sections of the female genital canal of his form which displayed a pronounced scarcity of nuclei. However, if one would examine the series of sections of which figure 34 is a sample, it would be seen that a full complement of nuclei are present and that in many places the cell-boundaries are quite evident. By examining figure 16, also of *Ph. highlandense* in which the female genital canal is cut in an almost perfect longitudinal section, it will be seen that the nuclei have

decreased in number [only one nucleus (*nu*) in this figure] and that the epithelium is in a decidedly frayed condition. Again, in many series of sections I have been unable to demonstrate even a single nucleus (figs. 12, 13, and 14, all from *Ph. kepneri,* are cases of this sort) and in others, only one or two nuclei have been found (see fig. 31, *nu*). By examining figure 13, it will be seen that all signs of the nuclei have disappeared but the fibrillar structure is still evident and the ends of the fibrils have become twisted together at their inner ends like the end of a fine paint brush. In figure 11, from a series of sections of *Ph. virginiana,* the retention of the fibrillar structure and the loss of the nuclei is also evident. In a recently prepared series of sections of *Ph. virginiana,* the proximal third of the female genital canal is lined by a definite columnar epithelium with distinct nuclei, while the distal portion as far as the superior genital atrium was completely devoid of nuclei and in a marked degree of degeneration. KENK, in a still unpublished paper on the triclads of Virginia, says: "It is remarkable that in fully mature animals much of the epithelium of the copulatory organs is 'depressed', viz. the nuclei of the epithelial cells are depressed into a deeper layer. This is true for the epithelium lining the male and common atria, the vagina (posterior part of the bursa stalk), and the coating of the penis." Is this loss of nuclei of the epithelium of the female genital canal another case of depression? It would hardly seem to be the case, as I have never been able to find any trace of these "depressed" nuclei. Rather, it would seem that with the advent of sexual maturity of the female organs there is a progressive degeneration of the epithelium of the female genital canal and that the fibrillae are more resistant than the rest of the cellular material and retain their identity long after the rest of the epithelium is disintegrated. Whether this disintegration is associated with the process of egg-formation and whether the epithelium may be renewed from time to time is a matter of conjecture. However, the renewal of this epithelium when once lost seems highly improbable.

I have been unable to locate the nuclei associated with the muscle fibers of the muscular tunic of the female genital canals of my forms. This, I suppose, can hardly be expected without making especial preparations by maceration for their demonstration. In sections, however, especially when fixed by BEAUCHAMP's fluid, the female genital canal appears to be covered with what appears to be cytoplasmic processes arising from the muscle fibers of the tunic (see figs. 12, 14, 16, and 31, *cpm*). The last figure (31) was drawn from material fixed in ZENKER's in which the processes show considerable shrinkage. In no case do these structures stain with any of the dyes that I have used, and in this respect can not be confused with the glands which open in great numbers into the female genital canal.

In the discussion of the "Geschlechtstrakt-Darmverbindung" of my forms, I have already made mention of the morphologic relation of the ductus genito-

intestinalis (when present) and the opening of oviduct into the female genital canal. In *Ph. virginiana* we found that the oviduct emptied into the female genital canal at the point of union between the valve-like structure, which is equivalent to the ductus genito-bursalis, and the female genital canal. In *Ph. kepneri,* the oviduct opens directly into the base of the stalk of the bursa (ductus genito-bursalis), as is distinctly shown in figure 27, *cd.* Finally, in *Ph. highlandense,* it was shown that the oviduct opened directly into the female genital canal at a point considerably distant from its proximal end (see fig. 16, *cd*).

The ovaries of these forms fail to show any distinctive characters which would distinguish them from the ovaries of other species of the genus. The ovaries are covered by a thin tunica propria with small, flat, darklystaining nuclei. This tunic extends beyond the distal end of the ovary and forms, in part, a spherical chamber filled with a granular secretion which was described by GRAFF (1911, p. 373, Pl. IV, fig. 3, *rs*) for *Ph. agassizi* as a receptaculum seminis (see figs. 28, 36, 37, 38, 41). LUTHER (1921, p. 23, 35, text-figs. 21, *gd*), on the contrary, with good reason describes this extension of the tunica propria of the ovary of *Ph. typhlops* and *Ph. typhlops subsalina* as an oviduct. Up to this point, as a matter of clearness and simplicity, I have spoken of the point at which the oviduct opened into the female genital canal. As a matter of fact, such a statement is not absolutely accurate. In all of my three forms, the oviduct does not empty directly into the female genital canal but forms with the common yolk duct a short common ovi- and yolk duct which opens in turn into the female genital canal. This condition is shown best in my figure 36 which was drawn from a series of sections of *Ph. kepneri.* The figure shows the distal end of the ovary and its associated ducts. It will be seen that the extension of the tunica propria, which has been called a germiduct by LUTHER, forms a short stalk (*od*), the oviduct proper, which is met by the common yolk duct (*yd*), containing yellow shell-substance (*ss*) and forms with it a common duct (*cd*) which opens directly into the female genital canal. At the point of junction between the oviduct and the common yolk duct opens a very characteristically branched unicellular gland (gl_2). I say unicellular gland because usually there is only one nucleus associated with the whole structure. On a few occasions I have found a second nucleus associated with the stalk but this nucleus may belong to the sphincter muscles which control its lumen. If we were to examine the whole series of sections in which this gland is shown, and of which figure 36 is a specific example, it would be seen that the gland in this particular animal is quite large (about three times as large as shown in the figure). The gland secretes a granular material which, together with the gland itself, stains very heavily with haematoxylin. This gland appears to be the source of the darkly-staining glandular material which not only fills the common duct but is found

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in the neighborhood of its point of entrance into the female genital canal, and which likewise very often fills the hemispherical area at the distal end of the extension of the tunica propria of the ovary. It seems remarkable that I can find no mention made of this gland which is so evident in my three species. However, LUTHER (1921, p. 23) says in regard to the yolk duct: "Seine Wandung ist dünne, doch finde ich in der Ruhelege einen dicken Belag von Sekret (Textfig. 7 S), der ein enges Lumen frei lässt." LUTHER may be referring here to the secretion of this gland. VEJDOVSKY (1895, Pl. V, fig. 34), in his figure of the reproductive organs of *Ph. unipunctata,* shows a series of unicellular glands which open at the junction of the oviduct and the stalk of the bursa intestinalis. Other somewhat larger unicellular glands are shown emptying ventrally to the oviduct at its place of entrance into the female genital canal. The latter glands are labeled "shell glands", while the former are not labeled at all. It may be possible that the former represents the branched, unicellular gland which I have described and that he erred in drawing an individual nucleus to each branch. In *Ph. virginiana,* this gland has a more fan-like appearance (see fig. 35, gl_2). In this particular instance I was able to distinguish lobes (*lb*) which were extended into the lumen of the oviduct and into the cavity formed by the extension of the tunica propria of the ovary. COGNETTI (1916) shows in his figure 21 large cells which almost occlude the lumen of this region but shows no exterior glandular extensions of these cells. Furthermore, he pictures these cells with well-defined nuclei, while it will be seen that no such nuclei are to be seen in my figure. My figure 35 also shows strong sphincter muscles (*sm*) surrounding the stalk of the gland, but no second nucleus could be found in this series of sections. In *Ph. virginiana,* as in *Ph. kepneri,* the opening of the common duct into the point of junction between the female genital canal and the ductus genito-intestinalis is surrounded by strong dilator muscles (see fig. 27, *dm,* for condition in *Ph. kepneri*). In *Ph. highlandense,* the condition is entirely similar to that of *Ph. kepneri* with the before-mentioned exception that the common duct empties directly into the female genital canal and not at the junction between the canal and the ductus genito-bursalis, and that a second group of glands (see fig. 16, gl_3) are associated with the common duct. Somewhat distally from the sommon duct open the so-called "shell glands" (see figs. 16, 28, 32, 41, and text-figs. 1, A, B, and E, *sg*) which differ little if any among my three species. Figure 32 was drawn from a transverse section through the female genital canal of *Ph. kepneri,* showing the entrance of these glands into it. LUTHER (1921, p. 26, Pl. I, fig. 9) mentions and pictures these glands and their point of entrance into the female genital canal of *Ph. typhlops.* He gives no description of the glands themselves, but his figure 9 shows their general character and their place of entrance into the female genital canal. By comparing his figure 9 with my figure 32, it will

be seen that according to LUTHER the "shell glands" of *Ph. typhlops* are much smaller and more shrunken in appearance. However, this shrunken appearance may be due to fixation as VEJDOVSKY's (1895) figures 38 and 39 show much plumper glands for this species. Furthermore, by examining my figure 32, there will be seen a secretory cell (*sc*), containing a granular secretion and staining darkly with haematoxylin, which is associated with the point of entrance of the "shell glands" into the female genital canal.

Associated with the female genital canal of *Ph. virginiana* and *Ph. kepneri* are further unicellular glands of very peculiar construction. Each of these glands possesses a single, large nucleus and a lumen continuous with the lumen of the female genital canal itself (see figs. 11, 12, 15, 18, 19, 27, 35, 37, and 41, and text-figs. 1 A and E, gc_1). The cytoplasm of these cells has the same fibrillae so evident in the structure of the epithelial cells of the female genital canal (see figs. 12 and 19, *fib*). In *Ph. virginiana* these huge unicellular glands are scattered irregularly over the female genital canal, giving it a peculiar warty appearance (see figs. 11 and 41, gc_1), but usually there are several somewhat larger cells of this type on or near the point of union of the female genital canal and the ductus genito-bursalis. In *Ph. kepneri* these cells are very large and are always clustered about the proximal end of the female genital canal at its point of union with the ductus genito-bursalis (see figs. 12, 15, 27, gc_1). Furthermore, I have never observed them at any other point along the female genital canal. In this form, therefore, they have become localized and give the female genital canal a very characteristic appearance even in the living animal (see fig. 6, gc_1). The function of these glands, each consisting of a single giant cell, is problematical. It will be noted in fig. 12, that while the epithelium of the female genital canal is markedly degenerate and that no nuclei are to be seen, the nuclei are present and the cytoplasm shows no mark of degeneration in these giant glandular cells although the series of sections from which figure 12 was drawn shows that the lumina (*l*) of these cells are confluent with the lumen of the female genital canal. In sections stained with MALLORY's triple stain after BEAUCHAMP's fluid, the fibrillae of the cytoplasm of these cells stain a brilliant red. Furthermore, fibers (*mf*) of the muscular tunic of the female genital canal involve these cells and possibly act as sphincters controling their lumina (see fig. 19). I have been unable to demonstrate any such structures associated with the female genital canal of *Ph. highlandense*, although I have frequently seen large nuclei (see fig. 16, nu_2) in the region of junction between the female genital canal and the bursa.

Another important group of unicellular glands, which as far as I have been able to ascertain have never been described, enter the distal third of the female genital canal. In *Ph. virginiana* they are in their simplest form (see fig. 41, gl_4), are relatively limited in their extent, and the duct of each gland

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pierces independently the wall of the female genital canal. These glands in *Ph. virginiana* stain a brilliant red in MALLORY's triple stain and in material fixed in GOLDSCHMIDT's fluid. In *Ph. kepneri* and *Ph. highlandense* these glands reach a relatively enormus development, at least under certain physiological conditions. Each individual gland consists of a large, pear-shaped body and an extremely long duct and secretes a granular material which stains a rich red by MALLORY's triple stain after ZENKER's fluid, and a pale blue after BEAUCHAMP's fluid. The ducts of these glands are collected into groups or sheaves and enter the female genital canal as such. Figure 31 B, a longitudinal section of *Ph. kepneri* drawn from material fixed with hot ZENKER's and stained by MALLORY's triple stain shows fairly well the extent of these glands. In this figure, tgl_4 shows a portion of these glands which was cut in transverse section through their bodies. Their structure would indicate a serous rather than a mucoid nature and their secretion is difficult to differentiate from the granular secretion of the granular secretory glands of the male copulatory organ (*gg*), in that it stains identically with it in sections stained by MALLORY's after ZENKER's. By following through the series of sections from which figure 31 B is a sample, it will be found that the gland-bodies (tgl_4) narrow down gradually into long ducts which enter the female genital canal in groups (see fig. 31 A and B, dgl_4). Where a group of the ducts of these glands are cut transversely as they enter the epithelium of the female genital canal, their lumina give the impression of a group of pin-pricks piercing the wall of the canal (see figs. 31 and 47, dgl_4). In figure 16 from *Ph. highlandense* may be seen groups of these ducts (dgl_4) which had been cut through by the microtome knife before they had entered the wall of the female genital canal. In figure 47 from *Ph. kepneri* (fixed in BEAUCHAMP's fluid and stained by MALLORY's triple stain, in which the sections of the glands themselves stain a pale blue) great bunches of these glands are seen clustering around the base of the female genital canal and transverse sections of two groups of their ducts (dgl_4) can be seen piercing the walls of the female genital canal just above the level of its junction with the superior genital atrium. That a profound chemical change is undergone by the secretion of these glands after its entrance into the female genital canal is indicated from sections stained by MALLORY's after ZENKER's, as in no case have I ever found a red-staining secretion within the lumen of the canal although such a red-staining granular secretion is evident within the lumina of the ducts where they pierce the epithelium of the canal (see fig. 31, A *s*). It is a very remarkable fact, that in serial sections, the mouths of the ducts where they open into the female genital canal appear to be occluded and, as a matter of fact, the extreme ends of the ducts seem to be actually rounded off. How the abundant secretions of these glands ever reach the interior of the female genital canal is a matter for conjecture (see fig. 31 B).

In addition to the above- described unicellular glands, a few small, widely-scattered gland-cells are also associated with the female genital canal (see fig. 41, *gl*).

THE MALE COPULATORY ORGAN.

GRAFF (1904—1908, p. 2269) says with reference to the male copulatory of the genus *Phaenocora:* "In der Dalyelliidengattung *Phaenocora* scheint bei manchen Arten als bleibendes, in das Atrium vorragendes cylindrisches Organ ausgebildet zu sein, wie z. B. *Ph. unipunctata* (Örst.) (Lippitsch 595, VIII, 16) und einigen andern, einer Chitinbewaffnung entbehrenden Arten. Bei manchen mit einer solchen versehenen Arten, wie *Ph. stagnalis* Fuhrm. (725, XI, 52), ist ein ähnlicher Penis vorhanden, bei andern fehlt jedoch im Ruhezustande ein Penis, und er wird ausschliesslich vertreten durch den Ductus ejaculatorius, indem dieser bei der Erection vorgestülpt wird. Die an seiner Innenwand vertheilten Chitinstacheln kommen dabei nach aussen zu liegen. Was die Art der Chitinbewaffnung betrifft, so handelt es sich bei *Ph. stagnalis* (Fuhrm.) um eine chitinöse Membran, 'die an ihrer unteren (distalen) Hälfte 2 μ hohe, pyramidale Stalchen trägt, deren polygonale Basis in kleinen Abständen der Membran aufgesetzt ist (725, XI, 53). In ruhendem Zustande is der grösste Theil der feinen Chitinbekleidung eingestülpt, wobei sich die Membran in mehrere Falten legt, so dass der Penis bei schwacher Vergrösserung mehrkantig erscheint. Der Penis liegt, vom Rücken des Thieres betrachtet, etwas links in einer Aussackung des Atrium genitale (p. 280). Bei den übrigen mit Chitingebilden versehenen *Phaenocora*-Arten haben wir es mit einzelnen längeren Stacheln zu thun, die bald in sechs Reihen grosser dornförmiger Stacheln, wie bei *Ph. rufodorsata* (Sekera), bald als gleichmässig zerstreute schlanke Haken, wie bei *Ph. typhlops* (Vejd.) (XXI, 22), bald in Gruppen verschieden geformter Stacheln und Haken, wie bei *Ph. anophthalma* (Vejd.), den Ductus ejaculatorius auskleiden und an der Aussenseite des als conischer Zapfen erigirten 'Penis' nach Vejdovský (769) folgendermassen angeordnet sind (XXI, 20 und 21). Es sind vier Längszonen von fein zugespitzten, an der Basis stark verbreiterten (hohlen?) und zur Spitze schwach gekrümmten Chitinstacheln (a—d), dazu eine Stachelumrahmung der Mündung (e) vier grössere, plumpe, isoliert auf der Dorsalseite stehende Stacheln vorhanden, welche mit einer linsenförmigen Basalplatte versehen sind und die Form der Hutzähne von Selachiern besitzen (a,—b)."

From the above quotation, it would appear that GRAFF divides the male copulatory organs present in the various species of the genus *Phaenocora* into two main groups: (1) those in which there is a permanent cylindrical penis which habitually extends into the genital atrium; (2) those in which there is no permanent penis but in which the evaginated ductus ejactulatorius

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acts as a penis during copulation. In the first group he includes all forms without a chitinous armament of the penis and some forms in which it is present. All the forms included in the second group, however, possess chitinous thorns or hooks which beset the interior of the invaginated ductus ejaculatorius. In this classification GRAFF has apparently taken no account of the fundamental differences in the structure of the various copulatory organs of the genus which on careful study would appear to have been derived from a common type which originally arose as a rather simple invagination of the epithelium and its associated musculature. In order to clarify my position, I will first endeavor to give a clear description of the male copulatory organs of my three species and then compare their structure with those of the other known species of the genus. In doing this I have taken the liberty of reproducing the drawings of the male copulatory organs of a number of the species from various authors, in order to help in the comparison of the forms involved. Unfortunately, some of the drawings are incomplete in their details while others are manifestly incorrect in their fundamental conceptions. I have therefore in some cases been compelled to judge by inference rather than by actual details as to the meaning of some of the drawings.

Fortunately the male copulatory organs of my three species happen to be of very diverse types, which fact has been of considerable help to me as a basis for comparative study.

In *Ph. virginiana* the male copulatory organ is small (about 80—90 μ in the resting condition). As the animals themselves average probably about 1 mm. in length, it, therefore, is about $^1/_{12}$ of the total length of the extended individual. Fundamentally, it consists of a sac within a sac (see figs. 41, 45, 58, 59, 60, and text-fig. 2 A, a, b, c). The ductus ejaculatorius bears no thorns or hooks and, therefore, should belong to GRAFF's first group in which there is a permanent cylindrical penis. Observations on some twenty-five serial sections and total mounts, however, reveal three cases in which there was no evagination of the ductus ejaculatorius and hence no "penis" (see fig. 44, an example from sections). Furthermore, it was found in observing the male copulatory organ in the living animal that even a very slight pressure on the cover glass would cause an evagination of the ductus. In many cases a slight pressure would not cause an immediate evagination but after several minutes of observation the ductus would suddenly and almost instantly be evaginated. It would seem that contradictions due to fixation often had the same effect, as in many cases the ductus shows varying degress of evagination in sections. It is quite evident, therefore, that there is no "permanent" penis in this species. Furthermore, BRAUN (1884, p. 230) found the penis of *Ph. balticum*, an unarmed form, in sections to be long, and in one case thrust through the superior genital atrium into the inferior genital atrium. He, however, expressed some doubt of this being a habitual condition. Again, HOFSTEN (1911,

p. 44) in his description of the copulatory organ of *Ph. gracilis,* another unarmed species, says that the penis is evaginated in both his sections but finds the musculature contracted and says that he does not know how the penis looks when invaginated. He, therefore, seems to think that the penis (ductus ejaculatorius) is capable of invagination in this species. In my species, *Ph. highlandense,* the ductus ejaculatorius, although armed with thorns, is always partially evaginated in all my sections but I have observed it the invaginated condition in the living animal (see fig. 61). The male copulatory organ of this animal will be discussed in its proper place. Furthermore, it would seem very unlikely that the penis would hang permanently in the superior genital atrium or even be extended into the inferior genital atrium as it would be in the way of the developing egg and also prevent the entrance of the penis of another animal. I feel that all the evidence tends to prove that there is no such thing as a permanent penis in the genus *Phaenocora,* and what has been reported as such has been due to a too universal reliance on the study of serial sections. Furthermore, in some species the ductus ejaculatorius may be very easily evaginated by even the slightest pressure, while in others it requires considerable pressure or it may even be impossible in some cases to produce a complete evagination of the ductus ejaculatorius by this method.

By referring to text-fig. 2 A, it will be seen that the male copulatory organ of *Ph. virginiana* consists of an outer pear-shaped muscular sac, inclosing a second muscular sac lined by a very thin epithelium with large flat nuclei which contains the sperms and granular secretion. This inner sac leads distally into a cavity (sc_1) in which sperms are often seen to collect. Distally the sperm cavity is continuous with a rather long, muscular ductus ejaculatorius (de_1) (see also figs. 41, 44, 45, 60, de_1). The space between the inner muscular sac and its confluent ductus ejaculatorius is filled with a material which was aptly termed by LUTHER (1921, p. 20), in his description of the male copulatory organ of *Ph. typhlops,* as a "Plasmamasse" (*pm*). The structure and significance of this "Plasmamasse" will be considered in detail in the discussion of the male copulatory organ of *Ph. kepneri.* For the present it

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Text-figure 2. Semi-diagramatic reconstructions of the male copulatory organs of *Ph. virginiana, Ph. kepneri,* and *Ph. highlandense* based on studies both from the living animal and serial sections.

A. *Ph. virginiana* (x 250): a, organ in resting condition; b, organ with ductus ejaculatorius partially evaginated; c, organ with ductus ejaculatorius completely evaginated.

B. *Ph. kepneri* (x 125): a, organ in resting condition; b, organ with ductus ejaculatorius partially evaginated; c, organ with ductus ejaculatorius completely evaginated; d, steriogram of a section of the ductus ejaculatorius when in the invaginated condition.

C. *Ph. highlandense* (x 125): a, organ in the resting condition; b, organ with ductus ejaculatorius partially evaginated; c, organ with ductus ejaculatorius almost completely evaginated.

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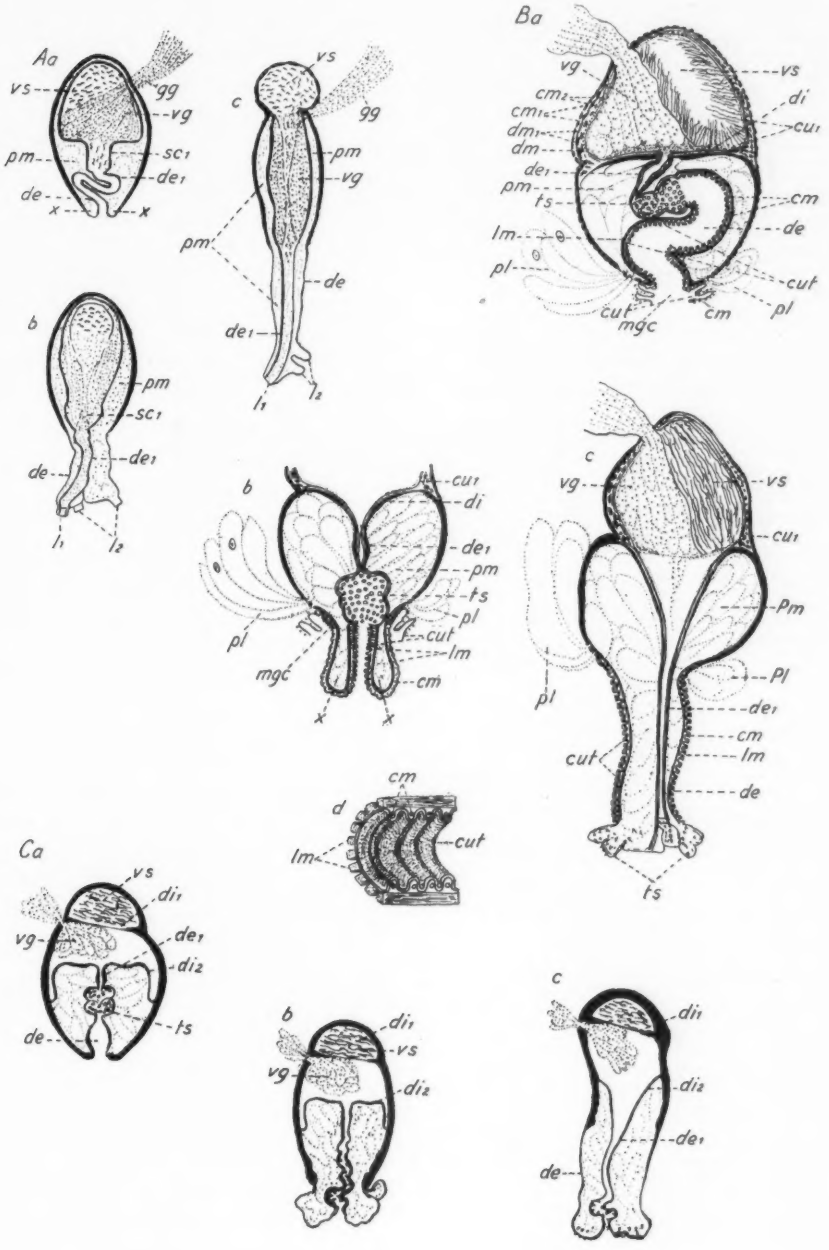

Text-figure 2.

may be described as a formless mass of plasma-like lobes (see figs. 41, 44, 45, 58, 59, 60, and text-fig. 2 A, a, b, and c). In copulation the contraction of the outer muscular wall of the copulatory organ compresses the "Plasmamasse". As the area *x*, *x* (text-fig. 2 A, a) is the weakest part of the organ, the "Plasmamasse" pushes this area downward and outward, gradually evaginating the ductus. As the proximal end of the ductus never becomes completely evaginated it becomes the definitive ductus ejaculatorius which carries the sperms and granular secretion during copulation (see figs. 40, 41, 45, 60, and text-fig. 2 A, a, b, c, de_1). As early as 1884, BRAUN (p. 230) recognized the probability of this mechanism in his description of the male copulatory organ of *Ph. megalops*. He says: "Wahrscheinlich ist es nun, dass bei der Begattung dieser Gang ausgestülpt ist, was die Contraktion der Muskelschicht des Penis bewirken wird, sodass dann eine einheitliche Leitung vorhanden ist." Text-figure 2 A, b shows the copulatory organ in a partially evaginated condition. It will be seen that the "Plasmamasse" has not only been pushed downward around the ductus ejaculatorius but has also been pushed upward around the inner sac housing sperms and granular secretion. The stretching produced by the pull of the ductus together with the compression due to the pressure of the "Plasmamasse" has elongated the sac but the sperm cavity (sc_1) is still evident and usually shows a considerable accumulation of sperms at this place. The distal end of the ductus ejaculatorius (*de*) now forms the outer wall of the so-called "penis". Strangely enough, the "penis" now assumes a very characteristic appearance. The distal end instead of being symmetrical is composed of three prominent lobes (see text-fig. 2 A, b, l_1, l_2) with the definitive ductus ejaculatorius opening at the end of the one most distally produced. As the evagination continues (see figs. 41 and 45) the "penis" becomes longer and longer while the two more proximally placed lobes become much smaller but are still very evident (l_2). While the number of these lobes is usually three, I have found as many as five in the study of one series of sections. When I first observed these lobes I took them to be artifacts, but I not only find them to be universally present in the evaginated "penis" in all my sections in which the "penis" is in the evaginated condition, but also in the living condition. I do not know what the function of these structures may be, but I suggest that they may form a mechanism which may prevent the "penis" from slipping from the genital pore of the fellow copulant during copulation. Furthermore, by examining fig. 41 and text-fig. 2 A, c, it will be seen that in this stage profound changes have taken place in the shape of the entire copulatory organ. Through the contraction of the muscular tunic of the outer sac the whole organ has become spindle-shaped and through a muscular constriction just above the entrance of the granular glands (*gg*) the sperms become confined in a temporary vesicula seminalis (*vs*).

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I have never been able to determine satisfactorily the plan of the musculature of the copulatory organ of this species. Its small size renders observation difficult and its pear-shape prevents a regular arrangement of the muscles, just as you would find it impossible to wind a cord regularly around a ball or a pear-shaped object. In general it may be said that the outer layer of the muscular tunic of the outer sac is composed of powerful muscles which have a general circular direction but often cross one another in a diagonal manner. These are by far the most powerful muscles of the organ but are not set very closely together but are separated from one another by a space equivalent to about their own breadth. Underneath this layer is a longitudinal layer of fine fibers. At the distal end of the organ where it is attached to the atrium superius may be observed rather closely set powerful longitudinal muscles. These muscles are unquestionably attached to the dorsal wall of the atrium but I have never been able to definitely determine their insertion. Where these muscles are attached to the atrial wall they are surrounded by powerful sphincter muscles which are undoubtedly an extension of the general outer layer of the sac. I can tell very little of the muscular complex of the inner sac and that of the associated ductus ejaculatorius. Sections show that the wall of the invaginated ductus is relatively thick (see fig. 44 de_1). In the evaginated condition (figs. 41, 45, 60), however, the muscles must become greatly stretched as the outer wall of the "penis" (de) appears very thin although the wall of the definitive ductus still appears quite thick (de_1). Judging by an analogy with the condition in *Ph. kepneri* the walls of the ductus in the invaginated condition should consist of weak circular and powerful longitudinal muscles, the latter undoubtedly assisting in the invagination of the ductus after copulation. At various places the inner sac is attached loosely to the outer by weak muscles. In fig. 44 *am* one of these places of loose attachment is shown. I have never, however, been able to see these places of attachment in the living animal or in total mounts. Two of these places of attachment are shown very distinctly in fig. 58, *am*, which is a transverse section of the proximal part of the copulatory organ in a partly evaginated condition. Fig. 59 from the same animal at a lower level of the organ shows no such attachment. As a matter of fact these points of attachment are very few. Inserted in the proximal end of the organ are powerful protractor muscles (fig. 41, pmu_1), and a second group of less powerful ones are inserted near the distal end, the fibers of which fan-out and are attached to the wall of the genital atrium (see fig. 44, pmu_2). These muscles probably serve the double function of orienting the position of the organ and pushing out the "penis" to its full extent during copulation.

The granular glands enter the copulatory organ together almost dorsally a short distance from its proximal end. At almost the same place enters the single ductus seminalis. There is no permanent division of the inner sac into

a vesicula seminalis and a vesicula granulorum and the sperms lie centrally and penetrate the peripheral mass of granular secretion (see figs. 58, 59, and text-fig. 2 A, b and c). This condition was reported for *Ph. megalops* by BRAUN (1884, p. 230) who says, "...der central Sperma, peripher und nach aussen Kornsekret enthält..." It is probably worthy of note that BEKLEMISCHEV (1929, p. 546) in summarizing the characters of the copulatory organ of *Ph.* (*Megaloderostoma*) *polycirra* which sets it aside from the copulatory organs of all other *Phaenocora*-species, gives as a fifth, though less important character, the opening of the granular glands into the bulbus near the entrance of the vasa defferentia. This condition is paralleled in *Ph. virginiana* only, instead of there being paired vasa defferentia there is a single ductus seminalis.

Associated with the base of the male copulatory organ where it is attached to the wall of the genital atrium are two groups of unicellular glands with very long ducts (fig. 41, gl_5 and gl_6). It is difficult to say whether they properly belong to the male copulatory organ or to the atrium superius as it would seem according to the position that their secretion would be discharged into the atrium. In addition to these glands scatterad small unicellular glands (gl_7) were found attached to the outer wall of the copulatory organ.

In *Ph. kepneri* the male copulatory organ is relatively enormous (about 300 μ in the resting condition). As the animals average about 2.25 mm. in length, it is, therefore, about $^1/_7$ the length of the extended individual. The copulatory organ (figs. 50, 51, 53, 54, and text-fig. 2 B, a, b, c, d) is a pear-shaped structure but differs fundamentally from that of *Ph. virginiana* in that it does not show the simple double sac-like structure exhibited by the latter. On the contrary it is divided by a muscular diaphragm (*di*) into a proximal bulbus, containing sperm and granular secretion, and a distal portion which, in the resting condition, contains the invaginated ductus and the "Plasmamasse". The ductus ejaculatorius of this form is divided into three very well defined sections. The most distal of these is lined with a very strong cuticula, which is thrown into very definite folds but bears no thorns (see figs 50, 52, 53, and text-fig. 2 B, a, b, c, d, *de*). Under high magnifications, it will be seen that the cuticula (*cut*) of this portion of the ductus is covered on the exterior with powerful longitudinal muscles underneath which are weak circular muscles which lie regularly in the folds of the cuticula (see figs. 50, 55, and text-fig. 2 B, a, b, c, and especially d, *lm* and *cm*). The median section of the ductus is a sac-like portion (*ts*) lined with thorns, in which both cuticular and muscular layers are much reduced. Finally, a proximal section (de_1), which becomes the definitive ductus ejaculatorius on evagination of the two former portions, that is lined with a thin cuticula and possesses both longitudinal and circular muscles. This definitive ductus ejaculatorius opens into the cavity of the bulbar portion

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of the copulatory organ through the center of the diaphragm and its cuticular layer is continuous with the cuticular layer of the diaphragm (cu_1), which in turn appears to be continuous with the basement membrane which underlies the very thin epithelium that lines the cavity of the bulbus.

LUTHER (1921, p. 20) remarked on the scarcity of nuclei associated with the "penis" of *Ph. typhlops*. He said: "Es ist bemerkenswert, dass in ganzen Penis i. e. S. oft kein einziger Kern zu finden ist." I also find it remarkable that this same condition holds for the "penis" of my three species. Where the nuclei are that should be associated with the extremely powerful musculature of the ductus ejaculatorius of *Ph. kepneri* is especially puzzling, as I have never been able to observe a single one. With reference to the "Plasmamasse", however, I was able to observe plasma-like structures bearing nuclei at the base of the male copulatory organ when in the living condition (see camera lucida sketch, fig. 53, *pl*) which later I was able to determine in sections to be continuous with the lobes of the "Plasmamasse" surrounding the ductus ejaculatorius. These continuations of the "Plasmamasse" pass through spaces between the muscles near the distal end of the copulatory organ (see text-fig. 2 B, a, b, c). Various authors (see under section entitled *Comparative Study of the Male Copulatory Organs of the Genus Phaenocora)* have described this packing tissue surrounding the ductus as connective tissue or as fine muscles. I am unable to offer any suggestion as to the nature of this tissue as all I know is that in the living condition it appears almost structureless, while in sections it does not stain readily with any stain I have used and appears as whorls of fine strands that have probably resulted from the shrinkage of fixation of the plasma-like lobes seen in the living condition (see figs. 50 and 51, *pm*). It certainly resembles neither connective tissue nor muscular tissue either in its appearance or its staining reaction. Furthermore, there seems to be no physiological necessity for either connective tissue or muscles in this locality, while a soft, plasm-like mass would be an ideal medium for transmitting evenly pressure exerted by the contraction of the muscular walls of the copulatory organ.

The ductus ejaculatorius is evaginated to form a "penis" in very much the same manner as in *Ph. virginiana,* only the proximal extension of the "Plasmamasse" is limited by the presence of a diaphragm (see text-fig. 2 B, b and c). In copulation, the diaphragm is drawn downward by the pull of the definitive ductus ejaculatorius until it becomes a funnel-shaped structure continuous with it (see text-fig. 2 B, c). The median, sac-like portion of the ductus, which is lined with thorns, on evagination becomes the distal lobed end of the "penis" (*ts*). I have never been able to determine how far the "penis" may be extended as it takes a great deal of pressure to evaginate the ductus in the living condition and it becoms partially retracted when the pressure is removed. In one case only have I seen the ductus even partially

evaginated in sections (see fig. 55), which is the reverse of the condition found in sections of *Ph. virginiana* and *Ph. highlandense*. I feel that the partial retraction of the evaginated "penis" on the release of pressure is probably due to inherent elasticity of the cuticula itself which tends to return it to its strongly folded condition. It is worthy of note that usually preparatory to the process of evagination the proximal part of the ductus becomes greatly shortened and the cuticula becomes closely folded so that the hitherto sinuous proximal section becomes a short, straight tube with strongly folded walls (see fig. 55 and text-fig. 2 B, b). By examining fig. 55, a drawing of the partially evaginated "penis", it will be seen that the folds are nearly straightened out where the pressure exerted by the "Plasmamasse" is the greatest but becomes folded again where the pressure is released. This is especially evident on the dorsal side of the partially evaginated penis in the figure. I am inclined to think that the folds of the cuticula become nearly if not completely flattened out in the fully evaginated condition. If so, the already long "penis" of this species must become very long indeed. The "penis" is probably retracted by the combined efforts of the longitudinal muscles of the proximal and definitive sections of the ductus ejaculatorius, the first shortening it and the latter, aided by a straightening of the diaphragm, actually invaginating it.

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VEJDOVSKY (1895, pp. 120, 121) says that the atrium superious takes the place of a vagina or, better still, a bursa copulatrix where the sperm stay for a time and only later are displaced into the spermatheca (bursa intestinalis) by means of convulsive contractions of the bursa copulatrix (uterus) and the ductus communis (female genital canal). It is quite true that I have often found sperm in the femal genital canal but I have never found any in the genital atrium. This, however, may have been a matter of chance. It seems to me, however, that the extremely long "penis" may be correlated with its very long female genital canal and that the "penis" may be thrust into the canal during copulation. It seems worthy of note that in *Ph. virginiana* in which the female genital canal is relatively long, the penis is also long, while the "penis" of *Ph. highlandense* (yet to be described) is short in apparent correlation with the short female genital canal of that species.

The male copulatory organ of *Ph. kepneri* does not open directly into the atrium superius but into a short male genital canal (figs. 50, 51, and text-figs. 1 E and 2 B, a and b *mgc*). In the living animal this canal sometimes becomes considerably stretched by the movements of the animal while at other times it may become greatly shortened. By careful observation, it will be seen that the cuticula lining the ductus ejaculatorius is continuous with the basement membrane (*bm*) underlying the epithelium of the genital atria and male genital canal which is, in turn, continuous with the basement membrane (bm_1) of the epithelium of the body. This is what might be expected

if VEJDOVSKY (1895, p. 114) was correct in his statement that the male copulatory organ is probably formed by an invagination of the musclesheath of the body.[1] If the cuticula lining of the ductus is a mere modification of the general basement membrane of the epithelium of the body surface, it would be reasonable to suppose that it would be associated with an extension of the epithelium, even though a basement membrane is commonly held to be a product of the parenchyma. I have diligently sought out such an epithelium in sexually mature individuals but was unable to find any trace of such. Finally, in one individual I found the ductus filled with a dark staining substance which on further investigation was found to be composed of a somewhat granular material containing many nuclei in various stages of disintegration (see fig. 52). It then occured to me that up to the time of sexual maturity the cuticula is covered by an epithelium which later on deteriorates, and that this dark staining substance containing nuclei is the product of its disintegration. Anyhow, I feel that this substance is identical with the "Stempel" of O. SCHMIDT which LIPPITSCH (1890, p. 161), suggested to be a mass of sperm.

GRAFF (1904—1908, p. 2269) indicates that the thorns of the ductus ejaculatorius of *Ph. stagnalis* (*clavigera*) are an integral part of the folded cuticula which lines the duct. In *Ph. kepneri* this is not the case as the thorns have an entirely different staining reaction than that of the cuticula to which they are attached. When stained with MALLORY's triple stain after saturated aqueous sublimate to which a few drops of glacial acetic acid had been added, the thorns take on a moderately deep red color while the cuticula stains a bright blue. In my species, however, the thorns are not set in the strongly folded portion of the cuticula but are confined to the sac-like portion in which the cuticula is greatly reduced. These thorns have a general pyramidal form but taper off into an elongated point. They are of two sizes. The larger measure about 3 μ in length, while the smaller are about 1.5 μ long.

The arrangement of the muscles of the male copulatory organ are somewhat more easily observed in *Ph. kepneri* than in *Ph. virginiana* (see fig. 50 and text-fig. 2 B). I have been able to distinguish four layers of muscles in the wall of the bulbus, while I have been able to discern but two in the distal portion housing the invaginated ductus ejaculatorius. This condition is easily explainable if one would consider the male copulatory organ of *Ph. kepneri* as derived from an organ of the type possessed by *Ph. virginiana* in which the sac containing sperm and granular secretion had become fused with the proximal portion of the outer wall of the organ. In *Ph. virginiana* we found that this sac was entirely independent of the outer wall or, at most, very lightly attached to it by a few weak fibers (see figs. 58 and 59). The result

[1] MEIXNER (1915, p. 538), however, states that the genital pore of *Ph. voriodentata* does not break through until after the reproductive organs are completely formed. This condition, however, may be secondary and peculiar to his species.

of an intimate fusion of the inner sac with the outer wall of the organ would result in an organ in which the bulbar portion, containing the sperm and granular secretion, would be separated from the distal portion by means of a diaphragm pierced at its center by the ductus ejaculatorius. One would expect, therefore, that the wall of the bulbar portion would be composed of both the muscles of the original outer wall of the organ together with the muscles of the sac, and that the muscles of the outer wall would be continuous with these of the distal portion of the organ. On examining the arrangement of the muscles it was found that the wall of the entire organ was covered by strong circular muscles (text-fig. 2 B a, cm_1), somewhat widely spaced, as in *Ph. virginiana*. Underneath this layer is another the fibers of which are not absolutely longitudinal in their direction but run somewhat diagonally (dm). Like the above mentioned circular muscles, this layer is continuous throughout the entire organ. These two layers would appear to be the original muscles of the outer wall of the organ of the type possessed by *Ph. virginiana*. Beneath these layers in the bulbar portion is a diagonal layer whose fibers lie at almost right angles with those of the preceding layer mentioned above (dm_1). This layer, however, ends at the diaphragm as would be expected if derived from the inner sac of the type of *Ph. virginiana*. Finally the inner layer of the bulbar portion is composed of fine circularly arranged fibers (cm_2) which likewise do not extend distally beyond the diaphragm. I have not been able to determine satisfactorily the arrangement of the muscles of the diaphragm but I expect that they are derived from the two inner layers of the bulbar portion which are, in turn, probably equivalent with the two layers of muscles of the invaginated ductus ejaculatorius. As mentioned before, the muscles of the invaginated ductus ejaculatorius consist of an inner, weak, circular layer and an outer, powerful, longitudinal layer. It will be noticed that they bear the same relationship with one another as the muscles of the atria and the muscular body sheath. This condition is entirely in accord with VEJDOVSKY's statement that the male copulatory organ of *Phaenocora* is formed as an invagination of the muscle sheath of the body. How the outer wall of the organ has been formed is, however, not so clear as it would seem impossible that the entire organ could be formed by such an invagination.

The granular glands (see figs. 50 and 51, gg) enter the bulbus from the dorsal side a relatively short distance from its proximal end. In some cases they seem to enter the bulbus side by side, but in others, especially when filled with secretions, they become slightly separated but are still very close to one another. The paired vasa deferentia unite to form a single ductus seminalis which enters the bulbus close to, and slightly proximally from, the entrance of the granular glands. LUTHER (1921, p. 18 and text-fig. 99) descri-

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bes the vas deferens of *Ph. typhlops* as opening into the vesicula seminalis through an elevated papilla. This, however, is not the case in *Ph. kepneri.*

The granular glands themselves vary greatly among different individuals both in appearance and extent. In some cases they are very voluminous and are filled with granules which stain a bright red with MALLORY's after ZENKER's or sublimate (see fig. 51, *gg*). In the animal from which fig. 51 was drawn, I found the extent of these glands to be relatively enormous, even extending dorsally at either side of the pharynx almost to the extreme dorsal side of the animal. FUHRMANN (1894, p. 275) found a very similar condition in *Ph. coecum* (*clavigera*) as he says: "Die accessorischen Drüsen des Penis, die zum Teil ganz der Peripherie des Körpers liegen, münden mit langen Ausführunggängen in den oberen Teil des Vesicula granulorum, die von der Samenblasen durch eine Membran getrennt ist." I have found in the "granulorum" and in the granular glands themselves hyaline string-like masses which stain a bright blue with MALLORY's (see fig. 51, *sm*). At first I supposed these masses to be of the nature of a connective tissue but further observation has led me to believe them to be a true secretion of the glands. These blue-staining strands seem to be entirely different from the cyanophil secretions described by GRAFF (1906—1908, p. 2249) in his discussion of the accessory glands of the rhabdocoeles. I have not only found this material in the granular glands of *Ph. kepneri* but also in those of *Ph. virginiana.* In other cases the glands and "granulorum" may be entirely devoid of red-staining granules and the glands reduced to little more than mere tufts. Under these conditions the "granulorum" assumes a net-like appearance (see figs. 50 and 63, *vg*). In this condition may often still be seen masses of the blue-staining material but never in any great quantities and are probably residual (see fig. 63, *sm*). The nature of this net-like structure is not altogether clear to me. It may be, and probably is, composed of the walls of the glands themselves which have been protruded into the lumen of the bulbus, but, however, is continuous with a mass of material of the same texture containing large nuclei but with no visible cell boundaries which covers the proximal side of the diaphragm in the region of the "granulorum" (see fig. 50). There seems to be no true granulorum as such but the sperm are separated from the granular secretion by means of a thin membrane.

I have not been able to demonstrate entirely to my satisfaction the homology of the glands that are associated with the base of the male copulatory organ and the male genital canal with those associated with the base of the male copulatory organ of *Ph. virginiana.* In fig. 31 may be seen a series of unicellular glands (gl_7) which lie on the ventral side under the female genital canal. I have traced the ducts of these glands back to the base of the copulatory organ in this series of sections and the glands themselves have a similar form and texture to that exhibited by the unicellular glands of *Ph. virginiana*

(see fig. 41, gl_5 and gl_6). There are, however, other unicellular glands associated with this region in *Ph. kepneri:* First, a group of unicellular glands of the same form and texture and staining reaction as those which empty into the distal third of the female genital canal (granules a dark blue with DELEFIELD's haematoxylin and light blue with MALLORY's after BEAUCHAMP's and red with MALLORY's after ZENKER's and sublimate). These glands are shown clearly in fig. 39, gl_4. Second, in the same figure (gl_8) will be seen a unicellular gland with a fine, granular net-like texture which stains weakly red with eosin after BEAUCHAMP's. This gland, however, may be identical with those of fig. 31 as I have been able to trace its duct back to the base of the copulatory organ.

Although *Ph. highlandense* is by far the largest of my three species, its male copulatory organ is only about 120 μ in length in the invaginated condition. As sexually mature individuals average about 3.5 mm. in the fully extended condition, the copulatory organ is about $^1/_{18}$ the length of the entire animal. It is, therefore, much smaller in proportion than the male copulatory organs of *Ph. virginiana* and *Ph. kepneri* which are respectively about $^1/_{12}$ and $^1/_7$ the length of the body. Several factors have made the study of the male copulatory organ of this species more difficult than that of either of the preceding ones. In the living condition, the natural opaqueness of the animal renders a minute observation of the organ difficult in the extreme. However, after the destruction of a large number of animals, I succeeded in making several quite satisfactory sketches of the organ both in the invaginated and partly invaginated condition (see figs. 61 and 62). I have never been able to find a fixing reagent that did not produce a partial evagination of the ductus ejaculatorius and a consequent contraction of the muscles that rendered the study of their arrangement next to impossible—a condition also observed by HOFSTEN (1911, p. 44) in his study of the male copulatory organ of *Ph.* gracilis. In the resting condition (see fig. 61, and text-fig. 2 C, a) the organ has the usual pear-shaped appearance characteristic of the genus but is sharply contracted proximally where the vesicula seminalis is shut off by a diaphragm (di_1) from a space which is in great part taken up by the granular secretion and may be spoken of as a granulorum. In my review of the species of the genus, I have only been able to find one other species in which there is a definite separation of the bulbus into vesicula seminalis and a vesicula granulorum, and that is in *Ph. anomalocoela* (see reproduction of HASWELL's 1906 figure in text-fig. 3 M, *vs*). The before-mentioned space, partly filled by the glands of the granular secretion, is bounded distally by a second diaphragm (see fig. 64 and text-fig. 2 C, a and b, di_2) which is pierced at its center by the ductus ejaculatorius (de_1). In sections (see figs. 56, 57, and 64, di_2), it will be seen that the diaphragm is attached to the wall of the copulatory organ a relatively short distance from the distal end of the same

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and is reflected proximally doubtless through the pressure exerted by the "Plasmamasse". In my figure 61, from a living animal, this diaphragm (di_2) appears to be attached close to the diaphragm (di_1) which separates the vesicula granulorum from the vesicula seminalis. This appearance is probably due to a further proximal reflection of the diaphragm so that the apparent points of attachment are only seemingly such, as the outer edge has been reflected back to such an extent that it appears to be a portion of the wall itself. This apparent discrepancy between the living and fixed condition is only what might be expected, as it is only in the living animal that I have been able to observe the fully invaginated organ.

From the above description, it will be seen that the male copulatory organ of *Ph. highlandense* differs from those of my other two species in two important features; namely, in that the vesicula seminalis and the vesicula granulorum are separated from one another by means of a definite diaphragm and that there is a marked space, only partly filled by the glands of the granular secretion, between the above-mentioned diaphragm and the penis proper. The first condition I find only among members of the genus *Phaenocora* in the species *anomalocoela* (see reproduction of HASWELL's 1906 figure of the male copulatory organ of that species, my text-fig. 3 M, *vs*). The latter condition is found among others in *Ph. typhlops* (see reproduction of LUTHER's 1921 figure of male copulatory organ in my text-fig. 3 G, a). By comparing LUTHER's figure with my textfigure 3 C, a, it will be seen that there is a certain similarity of structure between the male copulatory organs of these two animals, only that the vesicula seminalis is very small in my species, which, by the way, is associated with very small sperm in this animal, while in *typhlops* the vesicula seminalis appears to be very large as compared with the size of the organ as a whole. Furthermore, in my species there is a marked constriction of the proximal end of the organ, evidently produced by the pull of the proximal diaphragm. With reference to the ductus ejaculatorius there is a further less-marked difference in that the thorns are confined to a restricted area (*ts*) and are very much smaller in size than in *typhlops*. I have never been able to observe the copulatory organ of *Ph. highlandense* in a completely evaginated condition. Figure 62, from the living animal, and text-figure 3 C, c, however, show the organ in the nearly evaginated state. It will be seen that the thorns are confined to the extreme end of the evaginated ductus and that these thorns are of two sizes — the still unevaginated thorns being considerably larger than those that are already on the outer surface. In *Ph. typhlops*, on the contrary, the evaginated penis is completely covered by thorns (see reproduction of VEJDOVSKY's 1885 figure, my text-figure 3 G, b and LUTHER, 1921, p. 21, Textf. 10).

The ductus ejaculatorius is lined with a thin cuticula, which like that of *Ph. kepneri*, stains a bright blue with MALLORY's after fixation with

BEAUCHAMP's fluid, but is immeasurably thinner, so thin in fact that it is often difficult to detect. The vasa deferentia enter the vesicula seminalis very close together (see fig. 57, *vd*) but do not join nor open on a papilla as described for *Ph. typhlops* by LUTHER, 1921, p. 18, Textf. 8. The glands of the granular secretion enter the copulatory organ on either side of the vasa deferentia and at a level very slightly below them (see fig. 57, *gg*).

I have not been able to make a satisfactory study of the muscles of the male copulatory organ of this species as they have always shown a highly contracted condition in all my fixed preparations. By examining my figure 56—quite typical of all my preparations of this animal—it will be seen that the partly evaginated penis is thrust deeply into the inferior genital atrium. A similar condition holds for figure 57, although the inferior genital atrium is not shown in the figure. Apparently LUTHER found no such difficulty with reference to *Ph. typlops* as his figure 4 pictures the penis in a typical resting condition with no sign of evagination. By examining figure 56, it will be seen that the muscles labeled *mu* are in a high state of contraction. HOFSTEN (1911, p. 46) reported the same condition for *Ph. gracilis*. His figure is reproduced in my text-figure 3 C, a, in which similar muscles (*mm*) are shown in a similar state of contraction. HOFSTEN also mentions that his sections naturally do not allow him to show the condition of the penis in the uninvaginated condition.

I have no valid explanation to offer why the penis of some of the species of *Phaenocora* seem to be at least partly evaginated in sections, while in others this is not the case. I think it is well to point out here again, that if I had not studied *Ph. highlandense* in the living condition I might have easily supposed that this animal possessed a permanent penis and would fall naturally under GRAFF's first group (see pp. 318 and 319).

The Genital Atria and Pear-shaped Appendages.

I have already pointed out that the inferior genital atria of my three species lie posteriorly and slightly ventrally to the superior genital atria (see

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Text-figure 3. Reproduction of the figures of the male copulatory organs of various phaenocorans from the papers of various authors.

A. a. *Ph. unipunctata* from Lippitsch, 1890.
b. *Ph. unipunctata* from Vejdovský, 1895.
B. *Ph. megalops* from M. Braun, 1885.
C. a. *Ph. gracilis* from Hofsten, 1911.
b. *Ph. gracilis* from Vejdovský, 1895.
D. *Ph. jucunda* from Cognetti, 1914.
E. *Ph. vjatkensis* from Nasonov, 1919.
F. *Ph. salinarum* from Beklemischev, 1927.
G. a. *Ph. typhlops* from Luther, 1921.
b. *Ph. typhlops* from Vejdovský, 1895.
H. a. *Ph. vjatkensis* from Nasanov, 1919.
b. *Ph. vjatkensis* from Nasanov, 1919.
I. a. *Ph. vejdovskýi* from Vejdovský 1895.
b. *Ph. vejdovskýi* from Vejdovský, 1895.
J. a. *Ph. rufodorsata* from Hofsten, 1911.
b. *Ph. rufodorsata* from Hofsten, 1911.
K. a. *Ph. clavigera* from Hofsten, 1911.
b. *Ph. clavigera* from Hofsten, 1907.
L. *Ph. agassizi* from Graff, 1911.
M. *Ph. anomalocoela* from Haswell, 1905.

Labeling of the figures according to the various authors.

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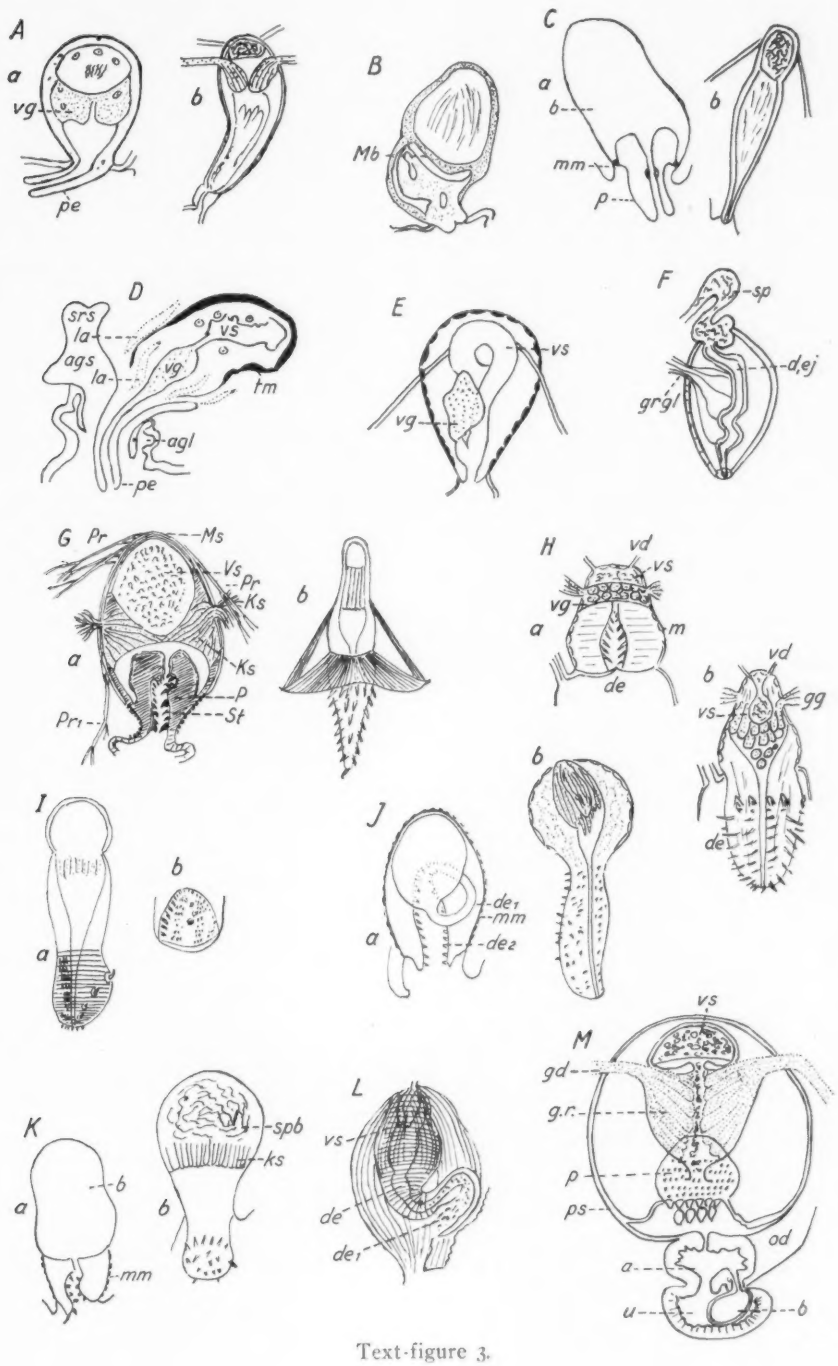

Text-figure 3.

text-fig. 1, A, B, and E), and that I am convinced that the decidedly ventral position of the inferior genital atria shown in the diagrams of several authors is due to the fact that these diagrams were reconstructed from the study of serial sections without a proper orientation of the relative position of the organs concerned from specimens in the living state.

VEJDOVSKY (1895, p. 114) stated that he is convinced that the genital atrium is formed as an invagination of the exterior of the body and that the male copulatory organ as an evagination of the atrium. My observations on mature individuals leads me to believe that his observations hold good for at least the majority of the species of *Phaenocora,* although MEIXNER (1915, p. 98) states that the genital pore of *Ph. variodentata* does not break through until after the reproductive organs are completed. My reasons for this belief are: first, that the basement membrane of the epithelium which covers the exterior of the body is continuous with the basement membrane of the epithelium of both inferior and superior genital atria and male genital canal, when present as in *Ph. kepneri,* which in turn is continuous with the "cuticula" of the ductus ejaculatorius, which in its turn is continuous with the basement membrane underlying the very thin epithelium lining the bulbus of the male copulatory organ. The relationships of these structures is shown quite well in figures 50 and 55, drawn from sections of *Ph. kepneri,* which, on account of the large size of its reproductive organs, lends itself particularly well to observations of this sort. Second, the arrangement of the muscles ensheathing the atria, male genital canal, and ductus ejaculatorius when in its invaginated condition corresponds with the arrangement of the muscle-sheath of the body: namely, epithelium, basement membrane, circular muscles, and longitudinal muscles (see fig. 50, *cm, lm,* bm_1, cu_1, *cut,* and text-fig. 1 B, a). It will be noticed that in figure 50 the epithelium of the superior genital atrium is degenerate and is not evident, while in figure 51 the nuclei of the superior atrium show clearly, although the epithelium itself does not show in cross-section. In this case, I suppose, the epithelium might be spoken of as "depressed". On the contrary, in all cases the epithelium of the inferior genital atrium is ciliated and shows no signs of degeneration.

Laterally, from either side of the superior genital atrium spring the "birnförmigen Lappen" or pear-shaped appendages which have been the subject of considerable discussion both as to their morphological significance and their physiological function. These structures, which are very characteristic of the genus *Phaenocora,* have been described at some length by several authors: notably, M. BRAUN (1885), VEJDOVSKY (1895), COGNETTI (1914), LUTHER (1921), and BEKLEMISCHEV (1929). Their structure does not vary to any observable extent among my species and judging from the descriptions of the above authors, their structure seems to be quite constant throughout the genus. I have been fortunate in getting several series of sections and one

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total mount which show the structure of these peculiar organs very clearly. Figure 41 is a camera lucida drawing from a total mount of *Ph. virginiana.* In this figure the penis is almost completely everted, and the nearly everted penis is thrust deeply into the superior genital atrium but the protractor muscles of the male copulatory organ (pmu_1) are only very slightly contracted, so that the penis has not been thrust beyond the confines of the superior atrium. It will be seen that the pear-shaped appendages are composed of two parts: namely, a part that is outside of the atrium (psa_1), and a part which lies within the atrium (psa_2). The cytoplasm of the cells that make up these organs is laminated. That these lamellae do not represent the individual cells themselves is certain as they far exceed the number of nuclei present. The bodies of these organs are made up of single rows of cells. The outlines of the lamellae which make up the cells appear crescent-shaped except in the area of the part which is contained within the atrium close to the constriction which separates it from the part which lies outside of the atrium in which the lamellae appear circular in outline. In the lobes which lie outside of the confines of the atrium, the points of the crescents point inward, while in the lobes within the atrium they point in the opposite direction. Furthermore, it will be seen that these cells must be of a very plastic nature, as the right-hand lobe conforms very closely to the shape of the penis, even filling in between the lobes (lb_2) which are so characteristic of the penis of this species. Now, it would seem quite certain that the outer wall of the penis can not be very firm as the cuticula covering it is extremely thin, so that the pressure exerted on the inner lobes of the pear-shaped organs must be relatively small. Nevertheless, the pressure exerted is sufficient to make the outline of the organ conform to the shape of the penis. If the penis had been completely everted, it would seem as if it would have been nearly or even completely surrounded by these plastic structures. As it will be explained later, this appears actually to be the case. Figures 46, 47, 48, and 49 were drawn from a series of sections of *Ph. kepneri.* In this animal, the penis was not everted, consequently the atrium is empty. From these sections it will be seen that the condition of the pear-shaped appendage is quite different from that described for the preceding case. The inner lobes (psa_2) are pulled outward, as it were, and no longer usurp the greater part of the cavity of the atrium. By examining figure 49, it furthermore will be observed that a large part of the inner lobe is no longer contained within the superior genital atrium proper but actually has been drawn outward by means of retractor muscles, of which one (*rmu*) is shown in the figure. It is also plain to see that this inner lobe is contained within an extension of the muscles ensheathing the atrium, while the exterior lobe (psa_1) lies outside of the muscle-sheath. We should now be in a position to understand what apparently takes place during the act of copulation: Coincidently with the evagination of the penis, there would appear to be a contrac-

tion of the protractor muscles (pmu_2), probably associated with a contraction of the muscular sheath surrounding the inner lobe, resulting in a pushing-in of the inner lobes into the atrium so that eventually their highly plastic cells surround the penis. In figure 40 (from a series of transverse sections of *Ph. virginiana*), it will be seen that these plastic lobes (psa_2) surround the penis laterally and ventrally, practically occluding the lumen of the atrium. In figure 45 from a series of sagittal sections of the same species, in which the penis is even more completely everted, the lobes have met even on the dorsal side of the penis and an examination of this series shows that they completely surrond it. In this particular case it will be seen that these plastic structures extend even into the inferior atrium.

In describing the above processes I have qualified my statements by using the expressions "there would appear", "probably", etc., as it must be borne in mind that the observations leading up to the above conclusions are observations of purely artificial conditions and possibly may not obtain in life. First, the evagination of the penis of the animal from which figure 41 was drawn was effected by pressure on the cover-glass; second, the evagination of the penis of the animals from which figures 40 and 45 were drawn was produced by contractions caused by fixation. I have, therefore, no certain knowledge of what actually occurs in the normal living condition. This much, however, may be said in favor of my hypothesis: In animals in which the process of fixation usually produces an evagination of the penis—as in *Ph. virginiana*—there is a coincident pushing-in of the inner lobes of the pear-shaped appendages into the lumen of the atrium, while in forms in which fixation does not normally cause an evagination of the penis—as in *Ph. kepneri*—there is no such pushing-in of these lobes. Furthermore, LUTHER (1921, p. 28) says with reference to the possible function of these organs: "Die Bedeutung der Organe bleibt nach wie vor dunkel. Soviel ist mir wahrscheinlich, dass vom proximalen Ende der 'Lappen' her Zellen unter allmählichem Heranwachsen gegen das Atrium verschoben werden, wobei sie sich mehr und mehr abplatten. Vielleicht werden so Polster gebildet, die dem fürchterlich stacheligen männlichen Glied bei der Begattung ein Widerlager bieten und nach etwaiger Zerreissung leicht wieder regeneriert werden. Zu Gunsten dieser Möglichkeit könnte es angeführt werden, dass ich bei einem Exemplar mehrere losgerissene (in Vacuolen eingeschlossene) Penisstacheln im Epithel des Atrium superius fand (vgl. Fig. 3)." From the above quotation, it would appear that LUTHER considers that these organs serve as "cushions" for the copulatory organ, but that these "cushions" are formed by a displacement of the cells by degrees toward the atrium, rather than by a contraction of the protractors and ensheathing muscles that force the lobes against the penis. However, the most significant part of the quotation relates to the fact that he found detached "Penisstacheln" in vacuoles in the cells of the pear-

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shaped appendages, which clearly indicates that these cells had been pressed tightly against the penis during copulation. For the above reasons, I feel that my interpretation of the behavior of these organs during copulation to be a correct one.

By referring again to figures 46 and 47, it will be seen that the lamellae of the cells of the pear-shaped appendages actually do not represent the cell-limits, as the cell-limits themselves are quite evident in these drawings. LUTHER (1921, pp. 26 and 27), in his description of these organs for *Ph. typhlops* says: "Am blinden Ende findet sich eine Anhäufung kleiner Zellen mit sehr chromatinreichen, manchmal zipfelförmig ausgezogenen Kernen. Mitosen habe ich hier nie finden können, halte es aber nicht für ausgeschlossen, dass in dieser Stelle eine direkte Kernteilung stattfinden könnte. Dieses Ende des Organs wäre dem Keimlager des Keimstocks zu vergleichen. Es folgt ein Abschnitt mit distalwärts immer stärker abgeplatten Zellen in mehr oder weniger ausgeprägt geldrollenförmiger Anordnung. Die Zellen scheinen sie sich gegen das Lumen des Atrium superius hin vorzudrängen, wobei der mittlere Teil der Organe nachgiebiger ist als äussere. So werden die Zellen buckelförmig distalwarts vorgewölbt. Es kommt aber auch manchmal vor, dass die buckelförmige Vortreibung in der umgekehrten Richtung stattfindet. Offenbar weicht das Innere der Zellsäule in der Richtung des geringsten Widerstandes aus, welche wechseln wird je nachdem sich die Kontraktionszustände von Hautmuskelschlauch und Atriummuskulatur ändern und in verschiedener Weise mit einander kombinieren." With the above statement, I most heartily concur but, in the cases under my observation, the inversion in the direction of the "hump-like fore-drawing" of the cells occurs at the point of union between the inner and the outer lobes which is situated at the outer end of the muscle-sheath and appears to be an area of considerable constriction. As these cells are very plastic, it is easily seen that their form would be displaced in opposite directions. In figures 46 and 47, it will also be seen that the "humping" of the most innermost of the cells has also been partially inverted, due probably to the pull against these cells exerted through the retraction of the lobes.

With reference to the cells which compose the outer lobes, which appear to be equivalent to those desribed by LUTHER as resembling "germinal layer of an ovary", I find that they may appear quite differently under certain conditions. In figures 41, 46, 47, 48, and 49, the cells making up the outer lobes appear to have the same lamellar structure as those making up the inner lobes, while in figure 43 and figure 44, A and B, they appear quite differently. Figure 44, B represents a highly magnified view of an external lobe of a pear-shaped appendage of *Ph. virginiana*. It was drawn from the next succeeding section to that from which figure 44 A was pictured. In this figure there is no indication of any lamellar structure of the cytoplasm of the cells and the whole structure is decidedly reminiscent of the germinal layer of an

ovary. In figure 43 (psa_1) this area shows an even greater division of the cells composing it, so much so in fact that it can no longer be considered as being composed of a single column of cells.

Figures 42 and 43 were drawn from a series of sections of a gravid *Ph. virginiana*. It will be noticed in these drawings that the inner lobes (psa_2) have been entirely withdrawn from the atrium and lie completely within a muscle sheath, the circular fibers of which (*cm*) are particularly evident. The more distally situated cells (*dc*) of the organ still exhibit their lamellar structure but the more proximally situated cells—those which are adjacent to the genital atrium—show marked signs of degeneration which seems to have progressed from the middle section inward, so that the cells (*pc* in fig. 42) have degenerated so much that they have completely lost their original form and appear as irregularly shaped fragments. The epithelium lining the atrium (*ep*), when evident at all, is extremely flattened and the parenchyma cells immediately surrounding it show a like flattening so that, as a whole, the tissues immediately surrounding the highly distended genital atrium appear lamellar-like in structure, the appearance probably having been produced by a combined stretching and pressing effected by the presence of a relatively large egg. Furthermore it will be noted that I have previously spoken of the division of the original single row of lamellar-like cells of the outer lobe into many smaller cells that no longer retain the lamellar-like structure of their cytoplasm. This would indicate that the cells of the lobe were in a state of rapid proliferation which I interpret as an attempt to replace the rapidly degenerating cells of the inner lobe.

LUTHER (1921, p. 27 and fig. 4, *Dr*) describes many small cells situated in the neighborhood of the blind end of the "birnförmigen Lappen" which have a club-shaped form and glandular appearance, staining very darkly with haematoxylin. He furthermore points out that it is not clear how their secretions arrive at the exterior as the "birnformigen Lappen" possess no lumina. BEKLEMISCHEV (1929, p. 533 and Abb. 10 and 11) describes similar cells associated with the appendages of the uteri of *Ph.* (*Megaloderostoma*) *polycirra*. I find habitually similar cells associated with the blind ends of the outer lobes of the pear-shaped appendages of all my phaenocoras (see figs. 41, 44 b, 46, 49 *glc*). However, I find that these cells vary as to shape, size, and staining reactions (see fig. 44 B, *glc*). Like LUTHER I am unable to suggest how the secretions of these cells arrive at the exterior.

With regard to the function of the "birnförmigen Lappen" I am taking the liberty of offering the following suggestions which seem to me to be in line with my morphological observations:

It seems reasonable to suppose that these organs may serve as a mechanism for the prevention of self-fertilization, as it appears that when the penis is evaginated the inner lobes of these organs completely fill such portions of the

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atrium that are not occupied by the penis itself, thus effectively shutting off all communication with the female genital canal. Against this may be objected that SEKERA (1906) remarks with reference to self-fertilization among the rhabdocoeles: "... wie der Inhalt der männlichen Samenblase weit dem Schwack ausgestülpten Penis ... durch den weiblichen Geschlechtsgang in das Receptaculum hineingespritzt wurde, so dass dadurch der untere Theil des Stieles angeschwollen erschien." However, I have never observed any such phenomenon among my species and I do not understand how it could be possible if I be correct in my supposition that the "birnförmigen Lappen" are habitually pressed in against the penis coincident with its evagination. I have never carried out any experiments in order to determine whether my phaenocoras will produce viable eggs either through parthenogenesis or self-fertilization, but I have frequently isolated for study individual phaenocoras from cultures in which large numbers of young phaenocoras were being produced and in no case did these isolated phaenocoras ever produce viable eggs. From these observations, which, however, can not be considered as controlled experiments, I am led to believe that not only no self-fertilization occurs among my species but that frequent copulation is required in order to insure fertilization, as I greatly doubt the ability of any sperms to get back into the female genital canal after once having arrived in the bursa intestinalis. CARTER (1929), however, reported that she raised a phaenocora from the egg to sexual maturity and that she observed moving embryos in the eggs of this animal but that they failed to hatch. This animal was supposed by her to be a *Ph. agassizi* but was actually a *Ph. virginiana*. During the fall and winter of 1932 efforts were made to repeat this experiment at this laboratory but this time *Ph. kepneri* was used as the subject of the experiment. Although a number of animals were reared from egg to secual maturity, when they produced a considerable number of eggs, in no case were embryos observed.

There is no question in my mind that the pearshaped appendages subserve some important function in the process of egg formation. That they serve as counter-beds to the frightfully thorned male member during copulation, as was advanced by LUTHER (1921, p. 28), does not seem probable. As a matter of fact LUTHER himself calls attention to the weakness of this supposition by admitting that other species of *Phaenocora* possess unarmed penes. BEKLEMISCHEV (1929, p. 533) suggests that they represent growth-zones for the regeneration of the epithelium of the uteri of *Ph.* (*Megaloderostoma*) *polycirra*. Again this seems hardly tenable. As a matter of fact it appears that the period of the degeneration of the cells of the pear-shaped appendages of my species is coincident with egg-formation and consequently with the degeneration of the epithelium of the genital atrium itself. At this period, the inner lobes appear to be entirely withdrawn from the atrium. If we

examine BEKLEMISCHEV's Abb. 10, a drawing of a section through the genital atrium and uteri of *Ph.* (*Megaloderostoma*) *polycirra,* it will be seen that the cells which form what I designate as the inner lobe of the pear-shaped appendage have the same lamellar structure as exhibited in my species. If we then examine his Abb. 11, which pictures the gravid uterus, it will be seen that these cells show the same erosion or degeneration as exhibited in my figures 42 and 43 only the degeneration does not appear to have gone quite so far and there is no indication of cell fragmentation. Why should these cells degenerate if they are to act in the near future as replacements for the degenerated cells of the atrium or uteri as the case may be? Taking everything into consideration this breaking down of the cells of the pear-shaped appendages must have some significance as yet unknown.

As to the morphological significance of these structures, I still feel that we are considerably in the dark in spite of BEKLEMISCHEV's statement that they represent rudimentary uteri, a supposition that had been expressed previously several times (BRAUN 1882, LUTHER 1905, 1921, BEKLEMISCHEV 1927). In short these suppositions seem to have been based in certain resemblances in the development of the uteri among the Typhloplanidae with the adult condition of the "birnförmigen Lappen" of *Phaenocora.* However, in spite of these resemblances, it seems that they can hardly represent such structures. According to BEKLEMISCHEV, *Ph.* (*Megaloderostoma*) *polycirra* possesses paired uteri, but from his drawings I judge that the pear-shaped appendages of these uteri are quite well developed and, barring very minor details, are quite as typical of the genus as those possessed by my three species. Furthermore, as I have already pointed out, they appear to subserve the same physiological function during egg-formation. How can these structures be rudimentary uteri in the case of *polycirra,* when *polycirra* actually possesses paired uteri? Again, can we rightly consider the possession of paired uteri to be more primitive in rhabdocoeles than the undifferentiated atrium serving as such? Is it not more logical to suppose that these organs are primarily, at least, associated with egg-formation and that their presence in association with the paired uteri of *polycirra* is quite in line with their functional activity?

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The Atrial Glands.

LIPPITSCH (1890, woodcut p. 156) pictures large unicellular glands (*dr*) with the atrium of *Ph. unipunctata,* but their ducts appear to enter the inferior rather than the superior atrium. VEJDOVSKY (1895, fig. 39 and 44) shows numerous, very large, club-shaped glands associated with the superior genital atrium of *Ph. typhlops.* In his figure 37 he shows a similar unicellular gland attached between the male copulatory organ and the "birnförmigen Lappen".

However, in his figure 34 of *Ph. unipunctatum,* he shows numerous small unicellular glands a single considerably larger unicellular gland associated with the atrium of the same animal. Of course the difference in the relative size of these glands may be due to a physiological condition, as the latter figure pictures the atrium shortly after copulation. However, the smaller glands of figure 34 appear much more numerous than the glands pictured in his figures 39 and 44. I have repeatedly found giant, unicellular glands associated with the superior genital atrium of *Ph. kepneri.* Many times they appear club-shaped—Indian-club-shaped, in fact—and decidedly resemble the giant cells of VEJDOVSKY's figures (see fig. 50, *agc*). At other times they may appear quite differently in sections but at all times they contain large, centrally-placed lumina which are confluent with the atrium (see figs. 39, 47, and 50, *agc*). These cells appear very similar in structure to the giant cells already described for the female genital canal, in that both types of cells contain large intracellular cavities and large nuclei but their cytoplasm shows no indication of the fibrillar structure so characteristic of the former. I do not find these cells to be as numerous as those shown in VEJDOVSKY's figures of *typhlops,* as I have never been able to count more than five of these giant cells associated with the atrium of any one animal. Curiously enough, two of these glands appear to bear some relationship to the "birnförmigen Lappen", as one of these glands is attached to the atrium on either side immediately above the pear-shaped appendages (see figs 39 and 47, *agc*). It is worthy of note that VEJDOVSKY (1895, fig. 37, *d*) shows such a gland in the same relative position in *Ph. typhlops. Ph. virginiana* also possesses atrial glands which are probably comparable to those described above for *Ph. kepneri* but differ considerably as to relative size and appearance just as the gland cells of the female genital canal differ in the two species (see figs. 11 and 44, *agc*). It will be noticed that the gland cell pictured in figure 44 is immediately above the "birnförmigen Lappen" as was also the case for *Ph. kepneri.* Under high magnification these glands also show lumina connecting with the atrium. Besides the above-mentioned glands, other much smaller glands are associated with the atria of the above two species. These appear to be of several types. Figure 39, agc_1 shows two very small unicellular glands which may be comparable to the small glands of VEJDOVSKY's figure. I know very little about the atrial glands of *Ph. highlandense,* as they do not show well in my slides and the living animal is so opaque that I have not been able to observe them clearly.

I have repeatedly searched for the "drüsigen Anhangsblase" of the atrium described by HOFSTEN (1911, pp. 42, 43) for *Ph. clavigera* and by LUTHER (1921, pp. 36, 37, and Textf. 18, 22, 23) for *Ph. typhlops subsalina* but I have never been able to find any such structure in my animals.

I have now completed the description of the reproductive organs of my three species. The rest of this paper will be devoted to a comparative study of the reproductive organs of the *Phenocora* species.

COMPARATIVE STUDY OF THE REPRODUCTIVE ORGANS OF THE PHAENOCORA SPECIES.

I. The Female Genital Organs and "Geschlechtstrakt-Darmverbindung".

Of the twenty-one described phaenocoras, the communication between the bursa intestinalis and the enteron has actually been observed in only eight forms: *unipunctata, typhlops, typhlops subsalina, jucunda, polycirra,* and my own three species, *virginiana, kepneri,* and *highlandense.* There is, however, no reason to suppose that such a communication does not exist in all the species, as it was not until 1909 that BENDL described a ductus bursa intestinalis for *Ph. unipunctata* and most of the species described before that date have received little recent investigation. However, considerable information may be gleaned from the descriptions of various authors with reference to the remaining parts of the "communicatio genito-intestinalis" (bursa intestinalis and ductus genito-intestinalis) and their relationship to the rest of the female genital organs. In interpreting these descriptions, the bursa intestinalis is of course quite evident and even at times the ductus bursa genito-intestinalis has, at least in part, been shown in figures without any realization by the author of its actual function, as in VEJDOVSKY's (1895) figure 46 of the female genital canal of *Derostoma anophthalmum* (*Ph. vejdovskýi*), in which the long, drawn-out portion of the bursa intestinalis (*rs*) unquestionably represents the ductus bursa intestinalis although the author had failed to observe its connection with the enteron. It also—with a few possible exceptions—seems fairly safe to assume that the "Bursastiel" of these authors is equivalent to the ductus genito-bursalis. By means of these descriptions together with the descriptions of the more recent authors who recognized the significance of the communicatio genito-intestinalis, and the study of my own species, I have been able to establish a morphological series which shows a tendency toward a shortening of the female genital canal coincident with a corresponding lengthening of the "Bursastiel" (ductus genito-bursalis), resulting, finally, in a complete suppression of the former, so that in some forms (*megalops, baltica*) the female genital canal is completely suppressed and the ductus genito-bursalis opens directly into the superior genital atrium without the intervention of a female genital canal. It also seems possible that there may be a second but more limited series in which there is a tendency for the opening of the oviduct into the female genital canal to migrate down the

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female genital canal toward the atrium, so that a false "Bursastiel" may be formed.

Text-figure 1, A, B, C, D, E, and F represent type-conditions of the reproductive organs of the *Phaenocora* species. In *Ph. virginiana* (text-fig. 1, A) the female genital canal (*fgc*) is moderately long; there is a short ductus genito-bursalis (*dgb*); and the bursa intestinalis (*bi*) opens directly into the enteron by means of a porous intestinalis. The oviduct or, more properly speaking, the common yolk and oviduct (*cd*), opens into the female genital canal at its point of junction with the ductus genito-bursalis. I have, of course, no means of ascertaining whether the ductus bursa intestinalis is wanting in the forms in which the communicatio genito-intestinalis has not been described but it appears to be present in all forms in which it has been described, but I must confess that in some cases the descriptions have been rather inadequate (BENDL's description of the "ductus genito-intestinalis of *Ph. unipunctata* for instance).

In the second type, exemplified by *Ph. kepneri* (see text-fig. 1, E), the female genital canal (*fgc*) is long; there is a very evident ductus genito-bursalis (*dgb*); and the ductus bursa-intestinalis (*dbi*) is also of considerable length. Like as in the preceding type, the common yolk and oviduct (*cd*) enters the female genital canal at its point of union with the ductus genito-bursalis. While the female genital canal is unusually long in *kepneri*, in general this arrangement seems to be the most common one among the *Phaenocora* species. This type appears to be applicable to *jucunda* (COGNETTI, 1915, figs. 25 and 27) and to *vejdovskýi* and *gracile* (VEJDOVSKY, 1885, figs. 42 and 46). VEJDOVSKY not only pictures but describes a pronounced stalk for the bursas of these two forms but, as I have already mentioned, furthermore pictures a long, attenuated part of the bursa which can be interpreted as nothing else than a ductus bursa intestinalis of considerable length. SEKERA's (1911, fig. 3) picture of the reproductive organs of *rufodorsata* also indicates a stalk for the bursa of that animal and the same holds good for HOFSTEN's (1911, fig. 8) diagram of the same species. I have, of course, no knowledge of a ductus bursa-intestinalis for *rufodorsata*, as nothing in the descriptions or figures of either SEKERA or HOFSTEN seem to indicate any such structure. The communication between bursa and enteron may, therefore, be a porus instead of a ductus and this species may belong to the first type rather than to the second. MEIXNER (1915, p. 541) describes the "receptaculum seminis" of *variodentata* as being composed of a broad ventral part and a narrow dorsal portion and also pictures the same (see his fig. 44). He thinks it possible that the dorsal portion (rs^2) may represent a ductus bursa-intestinalis which has not as yet broken through into the enteron and also considers that the somewhat widened proximal end may correspond to the "kanalartigen Blindsack" of *Ph. vejdovskýi*. To this group I am adding provisionally *Ph. achacorum*

on the ground of NASANOV's (1919, p. 1043) rather incomplete description of this animal, together with the appearance of these organs in his figure 2. Again, of course, I have no knowledge of a communication between bursa and enteron.

In the third type, as exemplified by *Ph. unipunctata* (see text-fig. 1, C), the female genital canal, according to the description of BRAUN (1884) and the figures of LIPPITSCH (1890) and BENDL (1909), is very short. The stalk of the bursa (ductus genito-bursalis) appears to be very long and the bursa intestinalis very little wider than the stalk itself. BRAUN (1884, p. 225) says with reference to these organs that near the penis stands a stalked bladder whose diameter only slightly exceeds the thickness of the stalk, and that for a long time he believed that the bladder discharged directly into the atrium, still it appeared to him in a preparation as if the oviduct is united with it shortly in front of its mouth. In LIPPITSCH's woodcut the female genital canal (labeled oviduct, *od* in his woodcut) appears somewhat longer than one would believe to be the case from BRAUN's description, but in BENDL's figure 2 the female genital canal (also labeled *od* in his figure) appears very short indeed—much shorter than in my text-figure 1, C. From BENDL's (1909, p. 298) description of the "ductus genito-intestinalis" of this species, I am inclined to believe that the communication between bursa intestinalis and enteron is probably in the form of a porus instead of a ductus as he says that the end-section of the duct which lies against the lumen of the gut appears to have been formed by a separate receding of the cells of the gut. However he may refer to transitional stages shown by cells forming a valvular apparatus as described by me for *kepneri* and *highlandense*. Nevertheless, his text-figure 2 would indicate that the communication (*dgi*) between the bursa intestinalis (*rec*) and the enteron (*D*) is very short, which helps to substantiate my belief that a porus is indicated rather than a ductus. In my text-figure 1, C I have shown the yolk duct as entering the posterior part of the genital atrium in accordance with BENDL's (1909) figure 2 and LIPPITSCH's (1890, p. 157) description and woodcut. There seems to be, however, some question where the yolk duct actually opens. In VEJDOVSKY's (1895) figure 34 of the reproductive organs of *Ph. unipunctata,* the oviduct is pictured as entering the female genital canal at the point of junction between female genital canal and the stalk of the bursa. Furthermore, the female genital canal (*dc*) appears relatively long and the stalk of the bursa quite short. It seems quite probable to me that the animal with which VEJDOVSKY was dealing was not of the same species as that from which LIPPITSCH and BENDL made their drawings. LIPPITSCH (1890, pp. 157, 158) has already pointed this out and suggests that VEJDOVSKY may have been dealing with either *baltica* or *megalops*. This can hardly be the case as the female genital canal appears to be nonexistant in the latter animale (see below), while in VEJDOVSKY's animal

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it is relatively long. I will admit, however, that it is possible that the female genital canal in VEJDOVSKY's figure was drawn in a highly extended condition as its lumen is shown almost entirely obliterated as probably the circular muscles of the duct were in a high state of contraction as indicated by the numerous constriction along the whole length of the canal but, even taking this into consideration, it would seem improbable that VEJDOVSKY's animal was identical with those of LIPPITSCH and BENDL. The question becomes still more confused as BRAUN (1884, p. 225) says that the common yolk duct of *unipunctata* lies where bursa and oviduct discharge. By this I take it to mean, at the point of junction between oviduct and *stalk* of the bursa. This condition would then appear to be identical with the condition described by VEJDOVSKY. However, BRAUN had previously said that in a preparation it appeared that the stalk of the bursa is united with the oviduct shortly in front of its mouth and that this condition may be comprehended as a receptaculum seminis hanging from the oviduct. I am inclined to think that what he designated as an oviduct must be in reality an extremely abbreviated female genital canal at the end of which both stalk and oviduct opens. However, he goes on to state that the short oviduct is surrounded by a ring of flat nuclei as by a follicular epithelium. The flat nuclei of the oviduct are most certainly characteristic of the oviduct of the genus but I must confess that I am entirely at a loss to comprehend how the stalk of the bursa could be attached to such a weak structure as the oviduct appears to be in this genus. As the matter stands today the position of the opening of the yolk duct in *unipunctata* must be left as an open question. To this group may finally be added *Ph. galiziana.* I have not read O. SCHMIDT's (1858) original description of this animal but GRAFF (1913, p. 138) states that the reproductive organs are similar to those of *unipunctata,* only that they lie entirely posterior to the genital pore. Of course again we are dealing with an animal of which we have no description of an actual communication between bursa and enteron.

In the fourth type, exemplified by *Ph. megalops* (see text-fig. 1, D), according to BRAUN (1884, p. 230) the uterus (superior genital atrium) receives directly the penis, bursa, ovary, and yolk duct. If BRAUN's description be correct, then it appears that the female genital canal is entirely wanting in this species and that the bursa intestinalis communicates with the atrium by means of the ductus genito-bursalis without the intervention of a female genital canal. Furthermore, with the loss of the female genital canal it would appear as if the common yolk duct has lost its connection with the oviduct and, therefore, no common yolk and oviduct is present. I am also including *baltica* in the same category as *megalops,* as I find only a slight difference in the arrangement of these organs in the two species. BRAUN (1884, p. 228) said with reference to the position of the bursa and oviduct of *baltica:* "Mehr nach hinten und ebenfalls dorsalwärts münden Bursa und Eileiter dicht

nebeneinander vielleicht durch dieselbe Mündung ein; die Bursa ist ein langer Kanal verläuft erst dorsal, dann im Bogen nach hinten." As he here speaks of the bursa as being a long canal which bends towards the rear, one might conclude from this that the opening of its communication with the enteron might easily lie at a point posterior to the genital pore, a condition found only in *galiziana* and *polycirra* among the other phaenocoras. Furthermore, BRAUN makes no mention of any enlargement of his "bursa" which might be considered as a true bursa intestinalis. However, the bursa intestinalis unquestionably varies very much in form dependent upon its functional activity and I do not think it advisable to doubt the presence of such an organ without further evidence. VEJDOVSKY (1895, p. 125) says that it appears highly doubtful whether BRAUN's species differ so much from one another that in the first the bursa and oviduct open in common into the uterus (superior genital atrium), as compared to separately in the other. As I interpret BRAUN's descriptions, however, it seems to me that BRAUN has shown very little difference as to the relative positions of the openings of bursa and oviduct, as in the case of *megalops* he says definitely (p. 230) in speaking of the "uterus": "... welch letzterer direkt den Penis, die Bursa, den Keimstock und die Dottergange aufnimmt", while in *baltica* he says that they open close to one another, perhaps through the same opening (see page 92). However, on page 231 he says with reference to the "bursa seminalis": "Die Bursa seminalis ist sehr lang, hufeisenförmig gebogen, ganz mit Sperma gefüllt und mündet seitlich neben dem Penis und etwas mehr nach hinten in den Uterus; ihr blindes Ende liegt dorsal über dem Uterus. An derselben Stelle mündet auch der Keimstock mit sehr kurzen Gang ein, so wie die vereinigten Dottergänge..." BRAUN (p. 228) seems somewhat in doubt as to the actual position of the opening of the common yolk duct of *baltica* but thinks it opens at the base of the bursa at a point where hangs a group of single cells.

VEJDOVSKY (1895, p. 119) states that a stalked bursa is a good systematic index of the *Derostoma* (*Phaenocora*)-species. In spite of this statement I can find nothing in either figures or descriptions of *typhlops, clavigera, anomalocoela,* or *vjatkensis* that would indicate that any of these forms possess stalked bursas. Therefore, it would appear that the ductus genito-bursalis is suppressed in these species. Naively enough, VEJDOVSKY refers his readers to his figures 34, 38, 46 *st* in substantiation of his generalization but fails to refer them to his figure 39 of *typhlops* which shows no definite stalk to the bursa nor is the constriction between the female genital canal and bursa, which might by a stretch of the imagination be considered as an incipient stalk, even labeled. LUTHER's (1921) text-figure 7, a schematic reconstruction of the reproductive organs of *typhlops,* shows no such structure, nor does his very complete description of this animal indicate that such a structure is characteristic or even occasionally present. The same holds good for both of

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HOFSTEN's (1907 and 1911) reconstructions of *Ph. clavigera* in which the bursa appears to arise directly from the female genital canal. Again, HASWELL (1905) does not show any stalk to the bursa in any of his figures of *anomalocoela,* nor does he mention any such structure in his description of the same. I am taking it for granted that no such structure is present in *vjatkensis* as NASONOV (1919, p. 634) states that the genital organs of his species resembles those of *typhlops* with the exception of certain details of the penis. It is, of course, questionable if he would have noticed what might have appeared to him such an unimportant thing as the presence or absence of a stalk to the bursa. In all the forms mentioned above the oviduct and yolk duct or the combination of the two appear to empty into the female genital canal at the point of its junction with the bursa intestinalis. On the strength of the above evidence, I have placed *typhlops, clavigera, anomalocoela,* and *vjatkensis* in a fifth group in which the ductus genito-intestinalis appears to be entirely suppressed.

According to STEINBÖCK's interpretation, the communicatio genito-intestinalis extends from the mouth of the oviduct to the enteron. This line of communication may be composed of three parts: the ductus genito-bursalis, the bursa intestinalis, and the ductus bursa-intestinalis. In *Ph. highlandense,* like in the preceding type (type 5), there is no ductus genito-bursalis, as the bursa communicates directly with the female genital canal without the intervention of a stalk (see text-fig. 1, B and fig. 16). It differs, however, from the preceding type in that the common yolk and oviduct (*cd*) does not enter the female genital at its point of junction with the bursa but has receded distally so that according to STEINBÖCK's definition the ductus genito-bursalis would be composed of a structure which is morphologically equivalent to the proximal portion of the female genital canal. That this portion of the female genital canal is not homologous with a ductus genito-bursalis is evident to any one who has examined either the living animal or serial sections of the same as it is histologically quite dissimilar. As I have not found this condition described for any other species of the genus, I have placed it in a group by itself—type 6.

GRAFF (1911) gives in figure 3 Taf. IV a representation of the reproductive organs of *Ph. agassizi.* In his figure he shows what he termed a bursa copulatrix (*bc*) at the end of a duct which is considerably larger in diameter than the bursa itself. This duct shows no evident variation in its diameter throughout its entire length and at its distal end, a short distance before it enters the atrium, is attached to the ovary by means of a short oviduct. GRAFF (1911, p. 373) evidently considered that this structure represents a bursa copulatrix to the stalk of which is attached the oviduct. His interpretation of these structures seems to me to be entirely untenable. In the light of my studies of my three species and the work of other authors, two plausible

explanations may be given for the structures involved: either a female genital canal reaches from the point of entrance of the oviduct to the atrium and from the entrance of the oviduct onward the continuation of the canal represents the stalk of the bursa (ductus genito-bursalis), or the whole duct is a female genital canal along which the opening of the oviduct has migrated distally until the ovary has become attached at its present position. If the first supposition be correct, then there should be a constriction just above the point of entrance of the oviduct and the proximal portion of the duct (the part between oviduct and bursa) should be histologically different from the distal portion (part between opening of oviduct and atrium). As a matter of fact, however, GRAFF (p. 373) describes the whole structure as possessing ringmuscles. In his figure, moreover, he shows not only ring- but longitudinal muscles both being very regularly arranged. If, on the other hand, the second supposition be correct then there would be no constriction immediately above the entrance of the oviduct and the whole duct would represent a female genital canal leading to a greatly shriveled bursa. Furthermore, the want of constrictions and the arrangement of the muscles is entirely typical of the female genital canal of the genus. If this last explanation be correct, which seems to be the most plausible one supposing GRAFF's observations to have been accurate, then we have another type in which the distal migration of the oviduct has been so great that the relative position of the oviduct is comparable to that exhibited by *Ph. unipunctata,* only that in the case of unipunctata this condition has been arrived at through a shortening of the female genital canal and a lengthening of the stalk of the bursa (ductus genito-bursalis), while in the case of *agassizi* there has been a simple migration of the ovary and its duct to its present position without any disturbance in the relation of the female genital canal to the bursa. Pending further information with reference to these structures in *agassizi,* I am giving *agassizi* a type value —type 7.

In the above discussion I have omitted all mention of the condition of the female genital organs of three forms: namely, *Ph. beauchampi, Ph. typhlops subsalina* and *Ph. (Megaloderostoma) polycirra.* Of the first (*beauchampi*), I have been unable to find any satisfactory description. As for *typhlops,* LUTHER (1921, p. 35) says: "... Das Rec. seminis und der Ductus-genito-intestinalis (*Dgi*) verhalten sich im allgemeinen wie bei *Ph. typhlops,* doch habe ich den Verschlussapparat nicht näher studiert." However, in his textfigure 18 (p. 34) he shows the communicatio genito-intestinalis as being quite different from the condition shown by him for *typhlops* in his textfigure 7 (p. 19), in that the bursa intestinalis (not labeled), or what I take to represent that organ, is very small and is separated from what appears to be a ductus genito-bursalis by means of a constriction. The lumen of the bursa, however, seems to be even smaller than that of the ductus genito-bursalis.

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While the proximal end of the bursa is guarded by ring muscles (*Rm*), it is, nevertheless, hard to determine because of the character of the drawing what constitutes the communication between bursa and enteron. It even seems possible to me that the whole structure may represent a true ductus genito-intestinalis without any bursa being present, the constriction spoken of above representing simply a temporary muscular constriction of the duct. For the present, therefore, I do not feel as if I am warranted in placing this form even provisionally among any of the types described above. I am in very much the same position regarding the condition of these organs in *Ph.* (*Megalodero-stoma*) *polycirra* as BEKLEMISCHEV (1929) gives very little attention to them in his otherwise very complete description of this species. In his text-figure 3 and in my diagramatic reconstruction of part of his figure (text-fig. 1, F), it will be seen that the whole communicatio genito-intestinalis is represented as an undifferentiated duct which though slightly swollen shows no sign of a bursa intestinalis as such. The entrance of the proximal end of the duct into the enteron is evidently guarded by a "Verschlussapparat" similar to that described by LUTHER for *typhlops,* COGNETTI for *jucunda,* and by me for *kepneri* and *highlandense.* Until further information is available, it is impossible for me to determine to which type this species belongs. With reference to the position of the female genital canal and communicatio genito-intestinalis in *polycirra* (see text-fig. 1, F), it is not so atypical as one might suppose at the first glance, as a mere posterior shifting of the attachment of the communicatio genito-intestinalis to the enteron is sufficient to account for this condition, which in no way involves a shifting in the position of the male copulatory organ as in *galiziana* in which both male and female genital organs lie posteriorly to the genital pore. I have already pointed out (p. 120) that according to BRAUN's description of *baltica,* the bursa, which he describes as being a long canal, bends toward the rear and that one might conclude from this that the communication with the enteron might easily lie posterior to the genital pore.

Below, I am giving a summary of the types discussed above and the species falling under each type. Forms in which a communicatio genito-intestinalis has actually been found are italicized. When descriptions have been so indefinite that there is a reasonable question as to the character of the communication between bursa-intestinalis and enteron, broken lines indicate the alternate possibility. I have also added whether eyes are commonly described as being present or absent in each form.

TABLE I.

I. Oviduct or common yolk- and oviduct at junction between female genital canal and communicatio genito-intestinalis or emptying into atrium when female genital canal is wanting:

A. Ductus genito-bursalis, bursa-intestinalis present; communication with enteron through a porus (Type 1):

virginiana	eyes present

B. Ductus genito-bursalis, bursa-intestinalis, and ductus bursa-intestinalis present (Type 2):

vejdovskýi	eyes absent
gracilis	eyes absent
achaeorum	eyes present
rufodorsata	eyes present
variodentata	eyes absent
jucunda	eyes present
kepneri	eyes present

C. Female genital canal greatly shortened with a coincident lengthening of ductus genito-bursalis. Communication with enteron probably either a very short ductus bursa-intestinalis or a porus (Type 3):

unipunctata	eyes present
galiziana	eyes present

D. Female genital canal medium to long but without a ductus genito-bursalis. A moderately long ductus bursa-intestinalis in *typhlops*. Condition in others unknown (Type 5):

typhlops	eyes absent
clavigera	eyes absent
vjatkensis	eyes absent
anomalocoela	eyes absent

E. Female genital canal wanting; ductus genito-bursalis very long; oviduct opening into atrium at same place as ductus genito-bursalis or separately but close to it. Type of communication with enteron not known (Type 4):

megalops	eyes present
baltica	eyes present

II. Oviduct or common yolk- and oviduct not at junction between female genital canal and communicatio genito-intestinalis but has migrated more or less distally from the junction:

A. Common yolk- and oviduct enters female genital canal about one-third distance between communicatio genito-intestinalis and atrium. Ductus genito-bursalis wanting, ductus bursa-intestinalis quite long (Type 6):

highlandense	eyes present

B. Distal migration of oviduct extreme. Apparently no ductus genito-bursalis. Communication with enteron not described. Opening of yolk duct doubtful (Type 7):

agassizi	eyes present

Doubtful group:

beauchampi	eyes present
Not described	
polycirra	eyes present
Not fully described	
typhlops subsalina	eyes absent
Not fully described	

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I must emphasize at thie point that the above groupings are only provisional as the desription of many of these forms are woefully incomplete and I suspect that some may be inaccurate as well. It seems to me that this genus has now grown to a size where a thorough review of the species would be advisable.

A morphological series such as I have described above for the genus *Phaenocora* has already been described for the genus *Dalyellia* by GRAFF (1904—1908, pp. 2324—2326). He says with reference to the female genital canal within that genus: "Nicht so einheitlich stellt sich der weibliche Genitalcanal bei den Dalyellinen dar. Namentlich die Gattung *Dalyellia* (Textfig. 78) zeigt, wie sich diese Ausstülpung des Atrium genitale allmählich herausbildet und einen bald kleineren, bald grösseren Bezirk der Wandung des Atriums umfasst. So fehlt bei *D. hallezii* (*D*) der Genitalcanal vollständig und das vom Atrium commune nicht scharf geschiedener Atrium femininum (*wgc*) nimmt alle die in Betracht kommenden weiblichen Organe durch gesonderte Mündungen auf. Wie hier der Stiel des Receptaculum seminis als canalartige Aussackung des Atrium erscheint, so geht bei *D. armigera* (*A*) eine solche bloss zum Germiduct, dessen distaler Theil hier als Receptaculum dient. Dagegen ist bei *D. scoparia* (*B*) und *viridis* ein Genitalcanal vorhanden, der in Gestalt wie Umfang complet homolog ist dem als 'Ductus communis' bezeichneten Abschnitte der Typhloplaninen." GRAFF (p. 2326) furthermore remarks: "Die Gattung *Phaenocora* (Textfig. 80) zeigt bis auf ihren längeren Receptaculumsteil grosse Uebereinstimmung mit *D. scoparia* . . ." GRAFF's text-figure 80 is a diagram of the copulatory apparatus of *Phaenocora* after a drawing by VEJDOVSKY (1895) but as far as the "Receptaculumsteil" is concerned, the stalk of the "receptaculum semininis" of *D. scoparia* which appears to be very short, or even wanting, as compared with the stalk of the "receptaculum seminis" (bursa intestinalis) of VEJDOVSKY's figure. Taking it all and all, it seems to me that the phaenocora diagram (text-fig. 80) resembles more closely the diagram of *D. viridis* (text-fig. 79 C) as to the relative length of the female genital canal, position of ovary and yolk ducts, and the fact that the receptaculum is stalked even though the stalk is relatively short. Be that as it may, it is quite evident that GRAFF was unaware that there was any morphological series in the genus *Phaenocora* in any manner comparable with that exhibited by *Dalyellia* and he probably thought that the condition shown in VEJDOVSKY's figure was constant for the genus. While I have not been able to find any condition in the genus *Phaenocora* in any way comparable with that in *D. armigera*, the condition in my type 2 approaches that shown by *D. viridis* (text-fig. 78, C), while my type 5, in which the stalk of the bursa is wanting, resembles that of *D. scoparia* (text-fig. 78, B), barring the position of the common yolk duct and the fact that a uterus is appended to the female genital canal. Again, the condition in my type 4, in which the female genital canal is wanting, is paralleled in the condition shown by *D. hallezii* (text-fig. 78, D)

or even more closely by *D. microphthalma* (see text-fig. 86, p. 2358 and footnote bottom of p. 2325) in which not only is the female genital canal wanting but the stalk of the receptaculum seminis is very long. It would seem, therefore, that conditions relative to the suppression of the female genital canal in *Phaenocora* is paralleled more or less closely in *Dalyellia,* including a coincident lengthening of the stalk of the bursa intestinalis in one case and the stalk of the receptaculum seminis in the other.

II. Male Genital Organs.

In previous descriptions of the male copulatory organs of *Phaenocora,* I feel that entirely too much emphasis has been placed on the presence or absence of denticles, their shape, size, number, and arrangement, and not enough emphasis on the fundamental structure of the organs as a whole. In making this survey of the male copulatory organs of the genus, I have been considerably hampered by incomplete descriptions and figures which, in some cases at least, are manifestly faulty, if not absolutely incorrect in one or more major details. By careful comparisons, however, of the descriptions and figures of various authors with the structure of these organs in my species, I have been able, provisionally at least, to place the male copulatory organs of the majority of the described species under three heads or types. In addition to these, I find two species (*subsalsa* and *polycirra*) in which the male copulatory organs as described seem to be atypical. Finally, I have been unable to find any description of the copulatory organs of either *galiziana* or *beauchampi.*

The male copulatory organ in its simplest form has a sac-within-a-sac structure, the outer sac being separated from the inner by the "Plasmamasse", with the inner sac housing both the sperm and granular secretion without any differentiation into a vesicula seminalis and vesicula granulorum. Such an organ I have already described for *Ph. virginiana* (see text-fig. 2 A, a). From some such simple condition appears to have been derived the more complicated organs of some of the other species. This type, therefore, I have designated Type 1. Under this category I have placed the male copulatory organs of *virginiana, unipunctata, baltica, jucunda, agassizi, rufodorsata, achaeorum, vejdovskýi,* and presumably *galiziana.* The condition in each of the above will be described below:

It is hardly necessary for me to mention again the male organ of *Ph. virginiana* as I have already described it in some detail in my description of the male genital organs of my species. As for *Ph. unipunctata,* it is only on most indirect evidence that I place the male copulatory organ of this species in this group as all descriptions are incomplete and the figures are unconvincing. Text-figure 3, A, a is a reproduction of LIPPITSCH's (1890) figure of the male copulatory organ of *unipunctata,* showing the penis in a partly evaginated

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condition. Neither LIPPITSCH's drawing nor his description indicates how this penis could be evaginated unless we can consider it to be constructed on a sac-within-a-sac plan similar to that which I have already described for *virginiana*. By this I mean that the outer, somewhat heavier line in the drawing may represent the highly muscular wall of the outer sac, while the inner, somewhat lighter line may represent the inner sac which houses the sperm and the granular secretion and is continuous with the still partly invaginated ductus ejaculatorius, and the space in between the two, the "Plasmamasse". Surely, the above-mentioned space could not represent a solid wall for, if the wall be solid, then there could be no possible mechanism by which the penis could be evaginated. It seems quite evident to me that LIPPITSCH's drawing represents a copulatory organ in which the penis has been partly everted through the process of fixation, which is fully in line with my observations in regard to the male copulatory organs of *virginiana* and *highlandense*. This supposition is strengthened by the fact that LIPPITSCH states that his study of the organs of *unipunctata* was entirely dependent on serial sections. Text-figure 3, A, b is a reproduction of VEJDOVSKY's (1895) figure of the male copulatory organ of what he supposed to be, and possibly was, the same species (see discussion of the female genital organs of unipunctata). However that may be, VEJDOVSKY was also evidently dealing with a copulatory organ built on the sac-within-a-sac plan, although the lines in the central part of the figure, leading from the granular glands to the opening at the distal end of the organ are not drawn either firmly or definitely enough to judge accurately of the actual structure. Furthermore, the structure at the distal end of the copulatory organ might easily be interpreted as a male genital canal although its walls appear to be unusually thick for such an organ. Unlike LIPPITSCH's figure, that of VEJDOVSKY was drawn from the living animal, so that in the first case we have a figure based entirely on serial sections, while in the second the figure has been based entirely on the living animal. In neither case, however, can it be said that the details are convincing. Both LIPPITSCH and VEJDOVSKY seem to be in agreement that the ductus ejaculatorius is entirely unarmed. BRAUN (1885) says very little about the structure of the penis of *unipunctata* except that it is pear-shaped and that the wall is composed of many crossing muscle layers, while the inner cavity is clothed by a clearly nucleated membrane. None of the above authors seem to have made any attempt to consider the structure of the penis of this form in relation to the possible mode of evagination. However, until further information is available, I feel justified in placing the male copulatory organ of *unipunctata* in my Type 1.

BRAUN (1885, p. 228) states that the penis of *baltica* is considerably longer than that of *unipunctata*, especially its "outgoing" part which projects as a long papilla into the uterus, in one preparation even as far as the atrium

inferius. His figure (Taf. IV, fig. 24), evidently from a section of this preparation, appears to have been drawn from a series in which the animal had suffered considerable distortion due to fixation. This is indicated by the almost vertical position of the penis and the sharp folding of the anterior portion of the wall of the superior genital atrium. I have frequently found a similar distortion in some of my preparations of my own species, as I have already pointed out in an early part of this paper. Furthermore, it would appear that the fixation could not have been of the best as the details of the structure are not clearly drawn. However, the section seems to have been made through a plane a little to one side of the median sagittal plane and has cut through the proximal end (the bulbar portion) of the penis but not through the ductus ejaculatorius. It would appear from the drawing as if this bulbar portion might be of a sac-within-a-sac construction and that the almost circular line might represent the wall of the inner sac. On page 230, BRAUN says in comparing the male copulatory organs of *baltica* and of *megalops,* in which the ductus is habitually carried in an invaginated condition in sections, that perhaps the ductus of *baltica* is also carried in an invaginated condition, and as he describes the process of evagination of the ductus of *megalops* as being effected by a contraction of the muscle-sheath so that a uniform pressure is exerted, it would appear that he probably considered that some such process took place in the case of *baltica.* Such a process could not take place if the penis possessed a single wall but is dependent on a sac-within-a-sac condition. As in the two previous cases, the ductus ejaculatorius is unarmed. In such cases as these, where the descriptions are incomplete, I have been forced to judge by analogy and it is very possible that my inferences may be incorrect.

Textfigure 3, D is a reproduction of COGNETTI's (1916) figure of the male copulatory organ of *Ph. jucunda.* The sac-within-a-sac structure of this penis is quite evident but again the organ has been drawn in the everted condition. There are several details of the drawing, however, which do not fall in line with what I would expect to find in a species of the genus *Phaenocora.* In the first place, the muscular outer wall (*tm*) is not continuous with the everted portion (*pe*). If this be so, then the condition in this form must be quite different from that described for any other species of *Phaenocora.* Such a structure would effectually interfere with the process of evagination as the "Plasmamasse" would be forced out through the hiatus between the distal portion of the muscular wall and the outer wall of the "penis". In the second place the possession of lacunae (*la*), not only in the area which should be filled by the "Plasmamasse" but outside of the muscular outer wall as well in the region of the parenchyma, is, to say the least, unusual. As a matter of fact, one is inclined to believe that these lacunae are nothing more or less than artifacts, produced in the process of fixation. Again, the area labeled *vg* (vesicula granulorum) seems to be comparable

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with the area labeled sc_1 in my textfigure 2, A, b of the partly everted penis of *Ph. virginiana,* which can hardly be spoken of as a vesicula granulorum although it often contains a portion of the granular secretion and sperms as well. Furthermore, I can not understand how a sagittal section through the superior genital atrium could cut through the "birnförmigen Lappen" (*agl*) in such a manner so as to cause them to appear in profile as they do in this drawing (see my discussion on the structure and function of these organs). As in the previously discussed species, the ductus ejaculatorius is unarmed.

In *Ph. agassizi,* we have another species in which the ductus ejaculatorius is unarmed. I have reproduced GRAFF's (1911) figure of the male copulatory organ of this species (see text-figure 3, L). Again, we have a drawing which is rather difficult to interpret. As a matter of fact the details of the figure are manifestly faulty. It will be seen by examining the drawing that the distal half of the inner part of the wall of the region of the ductus ejaculatorius (de_1) which forms the exterior of the definitive "penis" on evagination, is missing. Evidently, the organ is built on a sac-within-a-sac plan with the portions labeled de_1, *de,* and *vs* forming the inner sac while the lines exterior to the inner structure are probably meant to represent the walls of the outer sac with highly muscular walls. These features seem rather evident to me but I am at a loss how to interpret the long curved lines which seem to represent a third sac inclosing the other two. It may be possible that these lines represent protractor muscles of the copulatory organ, but protractor muscles would form straight lines and not curved ones. Furthermore, I can not make out the relationship of the distal end of the ductus ejaculatorius to the genital atrium. Altogether, the figure is anything but satisfactory and GRAFF's description does not help to clear up these discrepancies.

We now come to the description of the male copulatory organ of *Ph. rufodorsata.* Fortunately, HOFSTEN (1911) has given a very careful description of the male copulatory organ of this animal. Both his description and his figures, which I have reproduced (see text-figure 3, J, a and b), can easily be interpreted in the light of my conception of the fundamental structure of the male copulatory organ of a phaenocoran. This statement holds good not only for the description of the male organ of this species but also for his descriptions of the male organs of *Ph. clavigera* and *Ph. gracilis.* By examining text-figure 3, J, a the sac-within-a-sac structure is very evident and, as a matter of fact, differs very little fundamentally from the structure of the male organ of *Ph. virginiana,* as shown in my text-figure 2, A, a. There is the same almost globular bulbar portion of the inner sac which houses the sperm and granular secretion and the long ductus ejaculatorius and even the slight papilla-like projection of the ductus into the atrium mentioned by HOFSTEN (p. 35). The chief difference lies in the fact that the distal end of the ductus ejaculatorius (de_2) of *rufodorsata* is armed with thorns, while that

of *virginiana* is naked, and that a portion of the ductus ejaculatorius of *rufodorsata* lies in a coil back of the bulbar portion of the inner sac. Textfigure 3, J, b is a reproduction of HOFSTEN's drawing of the male organ in its evaginated condition. I am inclined to think that it is probable that the organ, as pictured, has not reached its maximum of evagination, as it is more nearly comparable with my textfigure 3, A, b of the partly evaginated "penis" of *virginiana* than with textfigure 3, A, c which shows the same organ at its most extreme evagination, in that the most proximal portion of the bulbar part of the inner sac is almost, if not quite, distinct from the outer sac. In my textfigure 3, A, c it will be seen that the extreme contraction of the outer muscular sac, aided by an undoubted sphincter area in the neighborhood of the entrance of the granular glands, has cut off the proximal end of the bulbus as a temporary vesicula seminalis, and that the close approximation of the outer muscular wall in this area with that of the proximal part of the bulbar portion of the inner sac is so complete that the double origin of this temporary vesicula seminalis would never be suspected while the male organ remained in its maximum condition of evagination. With reference to the material which occupies the space between the inner and outer sacs, HOFSTEN says that the broad space between the muscular outer wall and the true bulbus is filled with a connective tissue with a regular web. By this I suppose that he refers to the "Plasmamasse" which can hardly be spoken of as a true connective tissue but rather as a substance whose function is to transmit the pressure exerted by the contraction of the muscular outer sac in such a manner so as to accomplish the evagination of the ductus ejaculatorius. HOFSTEN also remarks that there is no separation into a vesicula seminalis and granulorum. This I find to be the case in all described phaenocoras with the exception of *anomalocoela* (of doubtful position) and my *highlandense* and possibly *variodentata*. Taking it all in all, I feel that HOFSTEN's excellent description of the male organ of *rufodorsata* would indicate that fundamentally the structure of the male organ is quite similar to that of my *virginiana* and that phylogenetically in all probability *virginiana* stands closer to it than to some other species in which the ductus ejaculatorius may be unarmed.

Textfigure 3, E, is a reproduction of NASONOV's (1919) figure of the male copulatory organ of *Ph. achaeorum*. Again I have to do with a figure that seems impossible of interpretation. The sac-within-a-sac structure seems clear enough although the curved "vesicula seminalis" (*vs*) is unusual. However, when we come to consider the vesicula granulorum and especially its position, one can not help doubting the accuracy of the drawing. If one examines the drawing, one will observe that the stalk of the granulorum is attached very close to the distal end of the ductus ejaculatorius. This same portion of the ductus is the part that must form the exterior of the "penis" when the ductus is evaginated during copulation. In this case it is quite evident that

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the granulorum must be carried with it which, on the face of it, is impossible. Again we have a species in which the ductus ejaculatorius is unarmed.

I am including in this group *Ph. vejdovskýi* although I must confess I have no good and sufficient reason for so doing as the only figure that I have been able to obtain of the male organ of this species has been drawn in the evaginated condition so that it is impossible to judge of the double-walled condition of the bulbar end of the organ, as I have already pointed out during my discussion of the male organ of *rufodorsata*. Text-figure 3, I, a and b are reproductions of VEJDOVSKY's (1895) figures of *Derostoma anophthalmum* Vejd. (= *Ph. vejdovskýi* Graff). It will be seen by examining these figures that there is nothing especially remarkable about them only the extremely short and wide distal portion of the ductus ejaculatorius which bears the numerous and various types of thorns with which it is armed.

Textfigure 3, M is a reproduction of HASWELL's (1905) diagramatic figure of the male copulatory organ of *Ph. anomalocoela*. The almost globular shape of the organ is unique within the genus — if *anomalocoela* should actually be included in the genus. Nevertheless the sac-within-the-sac structure is quite evident in the figure and is even more evident in HASWELL's fig. 33, plate 27 which was drawn from a serial section. In the latter figure the wall of the inner sac which incloses the granular secretions is seen to be much heavier than indicated in the diagramatic figure and appears to be continuous with the wall of the vesicula seminalis. The invaginated ductus ejaculatorius (*P*) is very broad and in this respect resembles that of *Ph. vejdovskýi* (see text-figure 3, I, b). Furthermore, the figure would lead one to suppose that the definitive ductus ejaculatorius indicated by the constricted end of the before-mentioned inner sac was not attached to the proximal end of the much broadened ductus which bears the thorns, but is attached to the side of the same. It is almost needless to state that this condition is hardly probable. HASWELL gives no figure or description of the appearance of the organ when in the evaginated condition but it would appear from its structure that the "penis" could hardly be very long. The actual occurence of a definite vesicula seminalis separated from a granulorum by means of a diaphragm is plainly indicated in the diagramatic figure and is confirmed in HASWELL's figures drawn from sections. With reference to the material filling the space between the inner and outer portions of the organ, HASWELL says (p. 458) that this space is filled by an "uncolorable substance" which contains a feltwork of fine filaments which he considers to be of a muscular nature. I judge by analogy that he is referring to a "Plasmamasse" and I doubt very much the muscular nature of these fibers. In his figure 33 these fibers are shown as irregularly coiled threads which seemed to have no definite points of attachment and it is hard to see how they could subserve a muscular function. I have frequently seen such a "feltwork" in the "Plasmamasse" of all my three species but in

no case have the fibers stained as muscles and, as a matter of fact, are as "uncolorable" as the rest of the "Plasmamasse".

The second type of male copulatory organ is exemplified by the male organ of my *Ph. kepneri*. I have already pointed out in my description of the male copulatory organ of this species that the bulbar portion, containing sperm and granular secretions, is separated from the distal half of the organ, which contains the long, coiled invaginated ductus ejaculatorius, by means of a muscular diaphragm, which is pierced in its center by the proximal end of the ductus ejaculatorius (see text-figure 2, B, a). I have also pointed out that I believed that this condition had been brought about by a fusion of the bulbar portion of the inner sac with the outer wall and that this supposition had been substantiated by a study of the layers of muscles inclosing the bulbar and distal portions of the organ. Furthermore, such a condition had been foreshadowed in the structure of the male organ of *virginiana* as scattered fibers had been observed which loosely connected the bulbar portion of the inner sac with the outer wall (see fig. 44, A, and fig. 58, *am*). The salient morphological feature of the male organ is, therefore, this muscular diaphragm which definitely divides the male organ of *kepneri* into a proximal and a distal part. Superficially, the long distal portion of the ductus, which is lined by the closely pleated cuticula and the area of thorns that come to lie on the exterior of well-defined lobes on evagination (see text-figure 2, B, a, b, and c), is the most remarkable feature of this organ, but does not possess the phylogenetic significance of the possession of the diaphragm and the fusion of the proximal portions of the inner and outer sacs to form a vesicula "granulo-seminalis".

I find only one other species of *Phaenocora* in which the male organ possesses the above-mentioned diaphragm and that is *Ph. megalops*. Text-figure 3, B is a reproduction of BRAUN's (1884) figure of the male organ of this animal. The general outline and appearance of this organ in the resting condition appears very similar to that of *Ph. kepneri*. The diaphragm (*Mb*), which BRAUN terms a membrane, although the term seems hardly applicable to such a decidedly muscular structure, is very evident and, furthermore, BRAUN notes in his description of the figure that this membrane is perforated by the ductus ejaculatorius. By examining the figure, it will be also seen that there is a considerable space which is not filled by the "Plasmamasse" but, however, this condition may be due to an artefact; the sections through the ductus ejaculatorius do not indicate that a thick, pleated, cuticle is present and the ductus is entirely unarmed. BRAUN has given no description of the muscular structure of the organ, but it will be seen that the wall of the proximal portion is much thicker than that of the distal portion which would indicate that the wall of the bulbar part has been formed by a fusion of the inner and outer sacs, as appears to be the case in *kepneri*. Judging by the figure alone, it would seem as if the structure of the male organs of these

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two species is essentially similar. However, BRAUN's (1884, p. 230) description leaves one in some doubt. He says: "... sein Bau ist anders als bei den übrigen Arten, da ähnlich wie bei manchen Mesostomen der Blindsack des Penis, der central Sperma, peripher und nach aussen Körnersekret enthält, durch eine dicke Membran abgeschlossen ist. Der lange, gewundene Ausführungsgang setzt sich nun nicht direkt an diese Scheidewand an oder ragt durch dieselbe in den Spermblindsach hinein, sondern beginnt mit einen offenen Lumen unter der Membran in einen Hohlraum; man kann sich diese Verhalten derart zu Stande gekommen denken, dass man, von einer Penisblase mit langem Ausführungsgang ausgehend, die Blase von dem Gang durch eine Querscheidewand, die an einer Stelle eine Oeffnung trägt, abgetrennt sein lässt und dann den Gang in sich selbst zurückgestülpen; so wird das periphere Ende desselben in die Nähe der Querscheidewand zu liegen kommen.

"Wahrscheinlich ist es nun, dass bei der Begattung dieser Gang ausgestülpt ist, was die Kontraktion der Muskelschicht der Penis bewirken wird, so dass eine einheitliche Leitung vorhanden ist."

By referring to the above quotation and comparing it with BRAUN's figure (text-figure 3, B), it will be seen that there is some discrepancy between the two. BRAUN says distinctly that the long, winding ejaculatory duct is not attached directly to the dividing wall or projects through the same into the blind sac containing the sperm, but begins with an open lumen under the membrane in a cavity. Nevertheless, in his description of the figure, BRAUN describes the transverse partition (diaphragm) (*Mb*) as being perforated by the ductus ejaculatorius, as I have already pointed out on the previous page. In spite of the discrepancies stated above, I feel quite certain in my mind that the structure of this organ is fundamentally similar to that of *kepneri* and can logically be placed in a group along with it. This conviction is strengthened as his conception of the process of evagination (see second paragraph of quotation) is entirely in line with what I have found to occur in *Ph. kepneri*.

In my Type 3, I have included the following species: *typhlops, vjatkensis, highlandense, gracilis, clavigera,* and *variodentata*. I am including the latter, however, with some reservations as it does not conform to the type in all respects and possibly should be placed in a type by itself. In Type 3 there is no indication of the sac-within-a-sac structure exhibited in the first type nor the muscular diaphragm of the second which can be easily derived from the first. I am selecting the male organ of *typhlops* as being representative of the group as LUTHER (1921) has made a very complete study of the structure of the male organ of this species. His figure (see text-figure 3, G, a) of the organ in the resting condition is very complete in its details. By examining this drawing it will be seen that there is a diaphragm pierced by the ductus ejaculatorius but that it is not noticeably muscular and does not divide

the organ transversely into two approximate halves as in Type 2. Furthermore, the diaphragm is attached very close to the distal end of the organ and is reflected backward proximally, so that the ductus ejaculatorius and the surrounding "Plasmamasse" inclosed within the diaphragm projects into a cavity lying under the granular secretion. Now, this diaphragm can not be thought of as being homologous with the diaphragm of Type 2 as the inner layer of muscles does not extend down to it and is not reflected over it as in the before-mentioned type. In other words: it would seem as if this diaphragm could not have been originally a part of the inner sac of what I have supposed to be the primitive type. Furthermore, I have no suggestion at present to offer as to their phylogenetic connection. Again, according to this diagramatic figure, it would appear as if the "Plasmamasse" (shown by diagonal hatching) extended up on the inside of the wall of the organ as far as the granular secretion. This condition is not substantiated by LUTHER's Fig. 4, Taf. I, drawn from a section, in which the peripheral edges of the diaphragm appear to be directly continuous with the muscular wall of the copulatory organ itself. Below this line of attachment, are shown only ring-muscles. However, it would seem as if there should be longitudinal muscles in this region as well, although they may be relatively weak and, therefore, not evident. I have chosen VEJDOVSKY's (1895) figure of the male organ of this species as an illustration of its evaginated condition (see text-figure 3, G, b) which agrees in all essential details with LUTHER's (1921, text-figs. 10 and 11) figures of the copulatory organ of the same species. In this figure it will be seen that the proximal end of the organ has become greatly reduced in size, so much so in fact that its diameter is even less than that of the original proximal end. Especially, it will be noted that the so-called vesicula seminalis has become greatly constricted and that the granular masses have become so greatly compressed that their axes lie parallel to the long axis of the organ itself. It would seem that the attenuated appearance of the organ in the evaginated condition is probably due to the fact that a considerable amount of contraction of the wall of the organ is necessary before any considerable pressure can be exerted against the "Plasmamasse" because of the cavity between the diaphragm and the granular glands.

Text-figure 3 H, a and b are reproductions of NASONOV's (1919) figures of the male organ of *Ph. vjatkensis*. It does not seem to me that this organ differs enough from that of *typhlops* to give the animal full species value on the basis of the male copulatory organ alone. The organ in its evaginated condition shows a striking resemblance to that of *typhlops*. As a matter of fact the organ as shown in NASONOV's figure resembles very closely in outline the organ of *typhlops* as drawn by LUTHER (1921, text-figs. 10 and 11, p. 21) which, in the evaginated condition, appears very much more robust than it does in VEJDOVSKY's drawing. Furthermore, NASONOV (pp. 334, 335)

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quotes VEJDOVSKY as saying that the ductus ejaculatorius of *typhlops* is equipped with spines of almost uniform length and thickness, while in his species the thorns are arranged in eight regular rows equally distributed over its entire surface, which are of several types. However, LUTHER (1921) did not find this to be the case and, as a matter of fact, found them to be of several sizes and shapes arranged in 5—7 more or less irregular rows. Be that as it may, I think the form and arrangement of the spines to be of small importance as compared with the fundamental structure of the organs concerned. The chief noticeable difference between the organ of this animal, as seen in the evaginated condition, and that of *typhlops* seems to lie in the appearance of the granular secretions which NASONOV describes as being made of club-shaped masses, while in *typhlops* they form strings. This appears to me to be of minor importance and may even represent a difference in physiological condition. NASONOV's figure of the male organ of *vjatkensis* in the unevaginated condition (text-figure 3, H, a), however, is markedly different from LUTHER's figure of the male organ of *typhlops* while in the same condition. It will be observed that the proximal end of the organ is decidedly contracted so that it already suggests the shape assumed by this part of the organ when in the evaginated condition. The base (distal end) of the organ appears very broad and there is no cavity between the diaphragm which is pierced by the ductus ejaculatorius and the granular secretions. On the whole, the appearance of the organ in this figure would suggest that the organ was in a state of partial contraction, great enough to obliterate the before-mentioned cavity, but not great enough to cause an evagination of the ductus. NASONOV also says that the space between the wall of the penis and the wall of the ductus is filled with muscles which retract the ductus. In other words, the space which is ordinarily occupied by the "Plasmamasse" is, in this species, occupied by muscles. NASONOV makes no mention of the methods he pursued in his investigations leading to the description of this species. I am inclined, however, to think that his observations were confined to the study of the living animal and that it is quite possible that the study of serial sections might fail to disclose the above-mentioned muscles. It seems to me that as the matter stands at present, the male organ of this animal while in the evaginated condition shows a remarkable structural resemblance to the male organ of *typhlops,* while, according to NASONOV's figure and description, the close resemblance fails when the organ is viewed in what NASONOV has described as the resting condition. I think it only safe to hold the recognition of the species in abeyance until more is known of its structural peculiarities and the methods by which they have been determined.

HOFSTEN (1911) redescribed *Ph. gracilis* from the same series of sections from which FUHRMANN (1894) described *Derostoma coecum* (= *Ph. gracilis* Vejd.). In general, HOFSTEN's description of the male copulatory organ fol-

lows rather closely that of FUHRMANN with the exception that FUHRMANN describes and pictures the ductus ejaculatorius as being armed with very small thorns while HOFSTEN declares such an armament to be wanting. In this, HOFSTEN is confirmed by VEJDOVSKY (1895) who studied the animal in the living condition. VEJDOVSKY's (1895) figure of the male copulatory organ is reproduced in text-figure 3, C, b. This figure gives very little structural detail and while evidently in the evaginated condition is not even thrust into the genital atrium. This is probably due to a want of contraction of the protractor muscles. HOFSTEN (p. 44) says that the evaginated penis is, as both VEJDOVSKY and FUHRMANN have observed, narow and of equal thickness. However, HOFSTEN's (1911) figure (text-figure 3, C, a) shows little resemblance to VEJDOVSKY's figure. As VEJDOVSKY's figure was based on the living animal, while HOFSTEN's is a reconstruction from serial sections, I feel that VEJDOVSKY's figure is probably more nearly correct than HOFSTEN's as far as the general outline is concerned. HOFSTEN says that in both the series of sections that he had at his disposal that the penis was evaginated though it is likely that it is carried invaginated in the resting condition as in the other species. However, by examining his figure (see text-figure 3, C, a) I am inclined to believe that it is only partly evaginated as the diaphragm is still reflected proximally and not drawn down to form a cone whose distal end is directly continuous with the definitive ductus ejaculatorius, as is shown in my figure of the evaginated penis of *Ph. highlandense* (see text-figure 2, C, c). Furthermore, HOFSTEN speaks of a long bulbus (b) which contains the sperm proximally and the granular secretion distally, but does not make mention of any space between the granular secretion and the penis *sensu stricto* as was found by LUTHER to be present in *typhlops* and by me to be present in *highlandense*. FUHRMANN's (1894, Pl. XI, fig. 52) figure, while somewhat more detailed than HOFSTEN's, confirms the position of both sperm and granular secretions but does not enlighten us as to the before-mentioned space. As a matter of fact, he has indicated what would appear to be a duct which leads from the cavity containing the granular secretion into the ductus ejaculatorius. In other words, the distal end of this duct appears to be thrust deeply into the proximal end of the ductus ejaculatorius. The presence of such a duct seems highly improbable. Both HOFSTEN and FUHRMANN show a thickening of the walls of the ductus about midway of its extent. It seems very probable to me that this thickened area would form the distal end of the penis in the fully evaginated condition. HOFSTEN remarked that he had considerable difficulty in studying the arrangement of the muscles of the copulatory organ as they were in a high state of contraction and I have already stated that I met with a similar difficulty in studying the muscles of the male organs of *Ph. highlandense*. It will be seen by studying the reproduction of his figure (text-figure 3, C, a) that he has indicated a particular group of

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muscles which are in a high state of contraction (*mm*). Such a group of muscles in a similar state of contraction I have often found in *Ph. highlandense* (see fig. 56, *mu*).

The structure of the male organ of *Ph. highlandense* is quite similar to that of *typhlops* with one important exception the sperm are definitely separated from the granular secretions by means of a diaphragm (see text-fig. 2, C, a, b, and c and figs. 61 and 64, di_1). This definite separation of sperm and granular secretion is only found in one other described species of *Phaenocora, anomalocoela*. This separation is indicated in the resting condition by a ring-like contraction near the proximal end of the organ (see fig. 61 and text-fig. 2, C, a and b). This condition may have come about by a further development of a simple sphincter such as was observed in *Ph. virginiana* (see text-figure 2, A, c). As I have before stated, I have never been able to observe the male copulatory organ of *highlandense* in the fully evaginated condition but, in the partially evaginated at least, there is no constriction of the proximal end of the organ as is seen in *typhlops* when the organ of that animal is completely evaginated. This is probably due to the extremely limited extent of the space occupied by the sperm in the case of *highlandense* as compared with *typhlops*. A consequent emptying of the space occupied by the sperm would not result in as great a reduction in the size of the proximal part of the organ as would be the case in *typhlops*. Of course the character and number of the thorns which compose the armament of the ductus ejaculatorius is quite different in the two species but, as I have said before, I consider this to be of secondary importance and, taking it all in all, the resemblances are considerably more important than the differences.

It is only with considerable reluctance that even provisionally I place the male copulatory organ of *Ph. clavigera* in this third group. In spite of HOFSTEN's (1911) rather complete description of the male organ of this species, I can not altogether visualize the structure of the male copulatory organ of this animal. I have reproduced his 1911 figure of the copulatory organ of the animal in its invaginated condition (see text-figure 3, K, a) and his 1907 figure of the organ in the evaginated condition (see text-figure 3, K, b). Both these drawings are rather incomplete and the first one does not entirely correspond with his description of the same. He says (p. 42) that the bulbus shows a weak constriction in the middle at the boundary between the sperm and the accessory secretion, and that outside of the bulbus is a shorter distal part. In its invaginated condition, he says, the latter forms a narrow ductus ejaculatorius to the walls of which are attached the thorns. The ductus is enclosed in its invaginated condition by a muscular sheath (*mm*) whose fibers are attached at their inner ends to the boundary of the genital atrium, while their other ends are attached to the bulbus about at the middle between the before-mentioned constriction and the beginning of the ductus

ejaculatorius. Now, by referring to the figure it would appear that these muscles were constrictors and consequently circular in disposition, while his description would lead one to believe that they were longitudinal and, consequently, would serve to shorten the "penis". This organ differs markedly from that of *gracilis, typhlops,* and *highlandense* in that there appears to be no backward reflection of the diaphragm which bounds the proximal end of the invaginated penis *sensu stricto.* Insomuch as this diaphragm must form a large portion of the definitive ductus ejaculatorius on evagination, it would seem quite evident that the evaginated penis must be relatively short, which seems to be in line with the facts (see text-figure 3, K, b). Furthermore, the decidedly pestel-shaped distal end of the evaginated ductus could easily be explained by a contraction of circular muscles rather than by the contraction of longitudinal muscles. Be that as it may, it would seem highly probable that both circular and longitudinal muscles are present, with probably the circular muscles being the more powerful. HOFSTEN gives no description whatsoever of the muscles of the bulbus which must be very important in producing the pressure required for the evagination of the ductus. In general, therefore, we may reconcile the plan of structure of the male organ of *clavigera* with that of the other members of this group if we consider the main difference to be represented by a decreased diameter of the diaphragm (which I am only postulating as HOFSTEN does not describe any such structure though of necessity there must be some sort of proximal boundary of the penis *sensu stricto*). Such a decrease in the diameter of the diaphragm would effectually prevent an in-pushing of the penis *sensu stricto* into the bulbar space and likewise limit the extent of the evagination of the ductus ejaculatorius.

As for the male organ of *Ph. variodentata,* I have already mentioned that MEIXNER (1915) described this species from two avowedly sexually immature specimens as the genital pore had not as yet established a communication with the atrium. I have not, therefore, reproduced MEIXNER's figure of the male organ of this species. His Figur 44, Taf. 31, however, would indicate that its structure is similar to that of *typhlops,* etc., in that the penis *sensu stricto* projects into the lumen of the vesicula granulorum while in the invaginated condition. In one respect, however, he shows a decided structural difference in that he states (p. 539) that there is a spacious vesicula seminalis separated from the granulorum by means of an epithelial fold. Finally, he states (p. 540) that he has erected this new species on the basis of the "thorning" of the "penis papilla" in contrast with that of *Ph. vejdovskyi.* This does not appear to me to be sufficient evidence for the establishment of a new species, as, as far as I have been able to learn, we know very little in regard to the actual structural make-up of the male organ of that species. As a matter of fact, I have already pointed out that what evidence I have been able to collect would indicate that the male organ of *Ph.*

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vejdovskýi is probably of a sac-within-a-sac structure. If this be so, then MEIXNER would have a decidedly more valid reason to consider this form to be a new species than mere differences in the "thorning" of the ductus ejaculatorius, which, from the meagre amount of material at his hand, may, after all, represent mere individual differences.

I do not intend to discuss in length the structure of the male copulatory organ of *Ph. typhlops subsalina* as LUTHER (1921) says that its structure is similar to that of *typhlops* although he was not able to observe it in the fully evaginated condition. His text-figure 18, however, shows the distal end of the unevaginated organ to be much more attenuated than that of *typhlops*. It is refreshing to be able to note that in spite of differences in the type and arrangement of the thorns and other minor differences both external and internal, that LUTHER has given this form only the value of a variety of *typhlops*.

I have now come to the discussion of the male copulatory organs of two forms which do not appear to fall readily within any of the three groups described above.

BEKLEMISCHEV (1927) described a form *Ph. salinarum* (Gr.) var. *subsalsa*. I have already noted that GRAFF (1913) had relegated this species among the Rhabdocoelida dubia as *Derostoma salinarum*. Text-figure 3, F is a reproduction of BEKLEMISCHEV's figure of the male organ of his form. By examining this figure it will be seen that there would appear to be no possible means of communication between the granular glands and the ductus ejaculatorius and, furthermore, the vesicula seminalis does not seem to be entirely enclosed within the walls of the organ. It is hard to visualize what would happen when the ductus ejaculatorius is evaginated. In the first place a weak place is left in the outer wall of the organ where the vesicula seminalis is not completely enclosed. With the contraction of the outer wall of the organ, the pressure of the enclosed "Plasmamasse" would tend to force the vesicula seminalis entirely out of the organ, while the pull of the ductus ejaculatorius in its process of evagination would tend to pull it in the opposite direction.

I now come to the discussion of the male copulatory organ of *Ph.* (*Megaloderostoma*) *polycirra* which from BEKLEMISCHEV's (1929) description appears to differ diametrically from that of all other described phaenocoras. Insomuch as the size of *polycirra* is relatively enormous (11 mm.), it would seem that the study of the organ should be relatively simple. I have not reproduced BEKLEMISCHEV's figure directly but have combined it in a diagramatic figure of the reproductive organs of his species (text-figure 1, F) which I have reconstructed from his figures 3 and 5. The male organ as shown in my reconstruction reproduces all of the essential details of BEKLEMISCHEV's figure. It will be seen by examining my figure that the organ is much more complicated and that not only is the cirrus (*cir*) armed with curiously

shaped denticles but that there are present as well many branched cirrulli (*ba*) which hang from the distal end of the organ and are retracted by means of muscles (*mu*). The question now arises, is the cirrus capable of invagination? If so, then it would seem that the invagination might be accomplished by a flattening of the diaphragm (di_b). If this should be the case, then the essential structure of the organ is similar to that of *megalops* and *kepneri*, only from the apparent fact of a want of a "Plasmamasse" between the diaphragm (di_b) and the distal end of the organ which is represented by a second diaphragm (di_a). However, the presence of this second diaphragm is in itself a disconcerting feature as it would seem that the surface represented by the diaphragm should be continuous with the outer or armed surface of the cirrus which should represent the invaginatable portion of the ductus ejaculatorius. Be that as it may, I feel that a further study of the male copulatory organ of this animal would reveal that it is not as so unphaenocora-like as might appear from a cursory inspection.

On the next page, I am giving a summary of the types discussed and the species apparently falling under each type. I am also, as in my table of the female organs of the genus, stating whether eyes are present or absent.

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One can not consider the table to be more than provisional in character, as in the case of the female genital organs the descriptions of the male organs in many cases have been anything but complete. However, some important facts may be gleaned by a study of the above table (TABLE II) and a comparison of this table with the one dealing with the female genital organs (TABLE I, pp. 349, 350), especially if one puts particular emphasis on the forms that have been carefully described for the structures in question. By examining Table I, it will be seen that there appears to be no significant correlation between the type of female genital organs and the possession of eyes. In the most common group (I, B) eyes are absent in three and present in four. In the remaining groups the frequencies are so small that any apparent correlation can not be thought of as significant. If we turn to Table II, however, there appears on first sight to be some correlation between the possession or absence of eyes and the type of the male copulatory organ. Under Type I (Male copulatory organ built on a sac-within-a-sac plan) I have listed ten species. In eight of these eyes are normally present, while in two (*vejdovskýi* and *anomalocoela*) eyes are wanting. Now if we take into consideration that I only included in this group the male organ of *vejdovskýi* with considerable reservations and that I had already in the introduction of this paper expressed a doubt as to the propriety of including *anomalocoela* in the genus *Phaenocora*, although I must admit that the male organ of the last is decidedly phaenocoran in all its important details, it will be seen that if it should be established that these two species should be excluded from this

TABLE II.

I. Male copulatory organ built on a sac-within-a-sac plan. Ductus ejaculatorius unarmed or armed (Type 1):

A. Ductus ejaculatorius unarmed:

virginiana	eyes present
unipunctata	eyes present
galiziana (presumably similar to *unipunctata*)	eyes present
baltica	eyes present
jucunda	eyes present
achaeorum	eyes present

B. Ductus ejaculatorius armed:

agassizi	eyes present
rufodorsata	eyes present
vejdovskýi	eyes absent
anomalocoela	eyes absent

II. Sperm and granular secretions separated from distal portion of organ, which contains a very long ductus ejaculatorius, by means of a muscular diaphragm. Ductus ejaculatorius unarmed or armed (Type 2):

A. Ductus ejaculatorius unarmed:

megalops	eyes present

B. Ductus ejaculatorius armed:

kepneri	eyes present

III. Penis *sensu stricto* may be retracted into space partially occupied by granular secretions. Ductus ejaculatorius usually short and straight. Ductus ejaculatorius unarmed or armed (Type 3):

A. Ductus ejaculatorius unarmed:

gracilis	eyes absent

B. Ductus ejaculatorius armed:

typhlops	eyes absent
typhlops subsalina	eyes absent
vjatkensis	eyes absent
clavigera	eyes absent
variodentata	eyes absent
highlandense	eyes present

Species in which the male organ can not readily be shown to fall into any of the above groups:

subsalsa	eyes present
Ph. (Megaloderostoma) polycirra	eyes present

Forms of which I have been unable to find any description of the male organ:

beauchampi	eyes present

group, then the correlation would be complete between the possession of eyes and the sac-within-a-sac structure of the male organ. In Type 2, which I feel, on the strength of my study of the male organ of *kepneri,* was derived directly from the more simple sac-within-a-sac form, both animals included within this group also possess eyes. Again, of the seven species included in Type 3, all are without eyes with the exception of one, *highlandense.* Now in this case there is no question as to the structure of the male organ or the propriety of including the form in the genus. Not only are eyes present but the body possesses a tail papilla characteristic of HOFSTEN's "Arten mit Augen und hinten zugespitzten Körper". Nevertheless, after reading LUTHER's (1921) description of the reproductive organs of *typhlops,* I was so impressed with their structural similarity to those of *highlandense* that I was for a long time in a quandary whether to consider *highlandense* a subspecies of *typhlops* or place it in a species by itself. Finally on consideration of its ramifying wing-like testes, distal migration of the common yolk- and oviduct, dorsal extension of the yolk ducts above the region of the pharynx, and possession of a definite vesicula seminalis, that I decided to give it species value. I have purposely left out of this list of differences the fact that the armament is confined to the distal end of the evaginated ductus ejaculatorius and the differences in the size and form of the thorns which make up the armament, as I do not feel that they are of species value. I will further add that the female organs are both markedly similar. Both have relatively short, thick-walled female genital canals; in both a ductus genito-bursalis is wanting; in both the ductus bursa-intestinalis is moderately long and is guarded by a quite similar "Verschluss-apparat". It was only the distal migration of the above-mentioned common yolk- and oviduct that differentiates the female genital organs with the exception of the yolk glands, of *highlandense* from those of *typhlops.* It will be seen from the above that *highlandense* as far as its reproductive organs are concerned resembles *typhlops* much more closely than it does any one of the species which possess eyes and have a similar form of body, and that *typhlops,* as far as its reproductive organs are concerned, resembles, with the possible exception of *vjatkensis, highlandense* more closely than it does any one of the "blinde Arten mit hinten verbreiterten Körper". From the above facts I feel safe in concluding that these two forms bear a very close genetic relationship in spite of their difference in bodily form and the fact that one does and the other does not possess eyes and, in partial support of this view, I quote HOFSTEN's own words: "Das sicherste Erkennungsmerkmal liefert der männliche Copulationsapparat." It might be well to recall at this time that the possession of a distinct vesicula seminalis is not entirely peculiar to the male organ of *highlandense* as among the species included in Type 3, MEIXNER (1915) described the sperm being separated from the granular secretions by

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means of an epithelial fold in *variodentata,* although the partition appears to contain muscle fibers in *highlandense.*

I am not attempting to deny that VEJDOVSKY's and HOFSTEN's division of the genus *Phaenocora* based on the presence or absence of eyes and on bodily form is of value as a key index for the identification of species but I do consider that these characters should be used with great caution in respect to the establishment of genetic relationship. I have already stated I have found "blind" individuals among my forms which normally possess eyes and the SEKERA (1904) found eyeless individuals among his *Ph. unipunctata,* which are described by some authors as having "diffuse" and by others as having "concentrated" eyes, and that he also found among his sketches a drawing of an individual with a broadened hind body after the manner of *Ph. vejdovskýi* which possessed eyes. Again, as recently as 1926, GIEYSZTOR found traces of eye pigment in *Ph. typlops,* which would indicate that eyes are potentially possible in that species. Furthermore, I have pointed out that it is actually the possession of a visual apparatus that makes for the presence or absence of eyes and not the mere presence of pigment where we conclude that eyes should be. Finally, have we any right to use the presence or absence of eyes as a specific difference? If through a mutation a race of men were produced who were without eyes and were otherwise as other men, would we be justified in calling the blind race a new species?

SEKERA (1904), on the other hand, suggested that all the phaenocoras with broadened body and penis beset with thorns be placed in a new species, *Derostoma* (= *Phaenocora*) *dilatum.* This division is by far not as absurd as it might appear to be without careful consideration. In the first place, SEKERA avoided the necessity of using the presence or absence of eyes as a specific characteristic. In the second place, he has likewise avoided the manifest error of considering the position, arrangement, size, and form of the denticles or thorns composing the armament of the ductus ejaculatorius as worthy of specific consideration. Furthermore, if you will examine my Table II, it will be seen that it will contain all the forms listed under III, B with the exception of my *highlandense*; and *vejdovskýi* and *anomalocoela* listed under I, B. The propriety of including the last two forms under I, B has been already discussed by me, so if we exclude these forms we will have a quite homogeneous group, all with broadened posterior bodies and with male copulatory organs that are structurally similar. Unfortunately, however, *gracilis* also possesses a broadened posterior body and the male copulatory organ, as I have already pointed out, is structurally similar, but according to HOFSTEN and VEJDOVSKY does not possess thorns and, finally, we can again hardly ignore *highlandense* whose reproductive organs, as a whole, are so similar to those of *typhlops* though the possession of a tail papilla would exclude it from this group. So

again we see another attempt to establish a homogeneous grouping of the species breaks down.

One can speak with less certainty with reference to a correlation between the type of female genital organs and the male organs than we could between the male organs and bodily shape or presence or absence of eyes, as in only a few cases has the presence of a communicatio genito-intestinalis been actually reported. Furthermore, it should be understood that the female copulatory organs are much more variable than the male, as they are much more subject to physiological differences which may be seasonal or otherwise. Insomuch as many of the investigators of this genus have confessedly worked with insufficient material—sometimes with not more than one or two specimens—it will be seen that great caution must be exercised in accepting irreservedly their opinions as to the actual structure of the female copulatory organs of the species they may have been working with. It would naturally be reasonable to suppose that there should be a quite definite correlation between the type of male and female copulatory organs but, strange to state (supposing my interpretation of the authors' descriptions to be reasonably correct) there seems to be very little or no such correlation. This will be made quite evident by a comparison of my Table I with my Table II. It is hardly necessary to take up these comparisons in detail but it might be well to take up one case as an illustration. Both *Ph. megalops* and *Ph. kepneri* have male copulatory organs of the same type, although in the first the ductus ejaculatorius is unarmed while in the latter the ductus bears thorns. In both forms the ductus ejaculatorius is very long and, consequently, the evaginated penis is likewise extremely long. Yet, when we come to compare their female organs the contrast is startling, for in *megalops* the female genital canal is entirely wanting, while in *kepneri* it is extremely long which would be as expected if I be correct in supposing the penis is thrust into the female genital canal during copulation.

With reference to a correlation between the type of male copulatory organ and the presence or absence of an armament of the ductus ejaculatorius, there appears again to be very little evidence of any such correlation. Of the ten forms listed under Type 1, in six the ductus is unarmed and in four armed; of the two forms under Type 2, the ductus is armed in one and unarmed in the other; and it is only in Type 3 that any correlation appears evident in which out of the seven forms listed only one (*gracilis*) possesses an unarmed ductus.

It will be seen from the above discussion that at least with our present state of knowledge that it appears impossible to establish any definite correlation between the structure of the male and female copulatory organs and the shape of body and presence or absence of eyes or even, as a matter of fact, between

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the structure of the female copulatory organs and that of the male copulatory organs. It appears to me, moreover, that the majority of the investigators of this genus have been so greatly concerned with such characters as the shape and arrangement of the thorns which form the armament of the ductus ejaculatorius, that they have failed to take cognizance of structures which were fundamentally more important in indicating genetic relationships. As a matter of fact in all the literature I have reviewed, not a single author has adduced any evidence to prove that the type of "thorning" is not a highly variable character or, at best, may be of only local application and could be considered worthy only as an indication of a sub-variety. After all, the mere multiplication of species without any realization of their phylogenetic position adds very little to our knowledge that can be considered really worth while. However, in order that we may arrive at this knowledge, it is necessary that we should obtain an accurate description of a large number of forms in order that we may make an intelligent determination of homologies. In order to do this the individual investigator must do something more than say this animal differs from that animal in one or more, more or less important characters, consequently it is a new species. On the contrary he should make such a thorough investigation of the form in question that a person desiring to make a comparative study of the group would have some accurate information to rely on. Such a description, moreover, can not be made from single or even a few individuals, as physiological and individual differences so often obscure the actual significance of the structures in question. It is, then, only through the contributions of a large number of individual investigators that the wealth of information necessary for the determination of the phylogenetic position of the forms in question may be arrived at. After all, what is a species? If any one has ever defined the term species satisfactorily, I have never heard of it. Neither is it of great importance to anyone except those who have a penchant for giving names to things—of importance only, when under the name of the species we can find a description which may be compared with another description under the name of another species, in assisting us in determining the history of the race and in forming an accurate basis for such experimental work as may be done upon the forms involved.

WITH REFERENCE TO THE SYSTEMATIC POSITION OF PHAENOCORA ANOMALOCOELA AND PHAENOCORA (MEGALODEROSTOMA) POLYCIRRA.

At best, any concept of a systematic term such as *genus, species* etc., can be nothing more than relative. Nevertheless, any investigator who has familiarized himself to any extent with a certain group, has a mental concept of

what comprises a genus within that group, which appears real enough to him although in reality it may be entirely artificial.

BRESSLAU in the *Handbuch der Zoologie* (1933, pp. 271, 272) recognizes three genera (*Phaenocora, Anomalocoelus, Megaloderostoma*) under a new subfamily, the Phaenocorinae. In other words, he has referred *Phaenocora anomalocoela* Graff (1913) back to *Anomalocoelus caecus* Haswell (1905) and has given the subgenus *Megaloderostoma* full generic value. However, in making these changes he gives no reasons or references.

In the introduction to this paper, which was written before I had seen BRESSLAU's survey, I had already questioned the propriety of including *anomalocoela* within the genus *Phaenocora*. This doubt I have re-expressed several times in the body of this paper. I have recently re-read HASWELL's (1905) description of this animal and the work seems to have been very thoroughly done and, furthermore, the paper is profusely illustrated with figures from sections and by diagrams. However, HASWELL fails to make any mention of the presence of the "pear-shaped appendages" so characteristic of the superior genital atrium of *Phaenocora*. Now this omission has been made by other authors in their descriptions of their species but I can not conceive of any one who has made such a careful study of his species failing to see such conspicuous structures as the "pear-shaped appendages" if such appendages were present. On this basis alone I feel inclined to sanction the removal of *anomalocoela* from the genus *Phaenocora*, for I can not conceive of a phaenocoran without the above-mentioned appendages. While this in itself is enough in my mind to effectually remove *anomalocoela* from the genus *Phaenocora*, what little information HASWELL has given us in regard to the excretory system leads me to believe that it also is very un-phaenocoran-like, in that he has neither mentioned nor pictured the large main stems, so characteristic of all other phaenocorans in which the excretory system has been described, which connect with the excretory pores that typically open slightly posterior to the middle of the ventral surface of the body. In that, as far as my experience is concerned, these main stems are the most conspicuous parts of the excretory system, it seems almost certain that HASWELL would have seen them if present. On these two features—especially the first one—I consider that BRESSLAU is justified in excluding *anomalocoela* from the genus *Phaenocora*.

As to the validity of giving *Megaloderostoma* full genus value, I feel that there is less justification. BEKLEMISCHEV (1929, p. 555) gives the following characters as separating *Ph.* (*Megaloderostoma*) *polycirra* from the rest of the phaenocoras: 1. the complicated form of the cirrus; 2. the female genital canal directed toward the rear; 3. the functional hollow uteri; 4. the presence of an independent dorsal section of the yolk glands. As a matter of fact, the female genital canal is directed toward the rear in *galiziana* and probably in

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baltica (see discussion of the female genital organs of *baltica*). Furthermore, such a change of the position of the female genital canal merely involves a posterior shifting of the opening of the communicatio genito-intestinalis into the enteron. Again, the possession or absence of uteri are not usually considered to be of generic importance among rhabdocoeles; vide: *Dallyellia*. Finally, dorsal extensions of the yolk glands exist in both *baltica* and *highlandense*, although I can not say that they can be considered independent. Of the above four characters, only the first seems to be particularly unique. BEKLEMISCHEV says (p. 546, 547) that the copulatory organ differs from that of other phaenocoras by a series of characters: (1) the presence of the cirruli; (2) the presence of muscle-retractors in the inside of the cirrus; (3) the presence of a muscular diaphragm; and (4) the presence of an epithelial lining of the proximal section of the ductus ejaculatorius. Finally, he adds a fifth character, which he considers to be of less importance, the entrance of the granular glands into the bulbus close to the entrance of the vasa deferentia. Of these characters the presence of cirruli appears to be absolutely unique. However, muscle-retractors of the "cirrus" have been reported for *vjatkensis* and *anomalocoela*, although I question the muscular function of the fibers present in the "Plasmamasse" of those animals. A muscular diaphragm is certainly present in *kepneri* and probably in *megalops*. As far as the epithelial lining of the proximal part of the ductus ejaculatorius is concerned, I have already pointed out in my description of the male organ of *kepneri*, that I am inclined to think that the ductus ejaculatorius, of that animal at least, is lined by an epithelium up to the time of sexual maturity. Finally, the granular glands and the vasa deferentia open into the bulbus of *highlandense* very close together (see fig. 57). In addition to this, the ramifying testes of *polycirra* are paralleled in highlandense. Taking it all in all I see no reason why *polycirra* should be given a generic or even a subgeneric value.

In concluding my discussion of the reproductive organs of this interesting genus, I want it to be distinctly understood that I do not consider there to be anything final in the conclusions that I have drawn. At best, I have but attempted to blaze a way for a more systematic study of the phylogenetic position of the animals composing the genus. If I be the least bit successful in this, I shall be extremely gratified. With this desire in mind I have included in this paper a relatively large number of figures and diagrams, so that other workers—especially European ones—might have the opportunity of comparing the reproductive organs of their species with those of mine, as any purely verbal description is, at best, unsatisfactory.

SUMMARY.

BRESSLAU (1933, p. 271) gives the characters of the subfamily Phaenocorinae as follows: "Typhloplanidae mit dorsal von den stark verzweigten und vielfach miteinander anastomosierenden Dotterstöcken gelegenen Hoden. *Bei starker Verzweigung breiten sich die Äste der Vitellarien auch dorsal über den Hoden aus.* Die beiden Excretionsendstämme münden mit getrennten Poren an der Körperoberfläche. Der Mund in die Nähe des Vorderendes, die Geschlechtsöffnung vor die Körpermitte verschoben. Der Schlund erinnert durch seine mit der Verlagerung nach vorn verbundene Schrägstellung und durch die Anordnung seiner Muskulatur an den Pharynx *der Dalyelliidae.* Der häufig mit Kutikularstacheln versehene Ductus ejaculatorius zirrusähnlich vorstülpbar. Mit Communicato oder Ductus genito-intestinalis."

I can not agree with BRESSLAU that ramifications of the branches of the yolk glands which extend dorsally above the testes is characteristic of the phaenocoras as a whole. As a matter of fact I consider this condition unusual rather than usual. There is one characteristic, however, that should most certainly be added to the above list and that is the possession of the "pear-shaped appendages" of the atrium. As far as i have been able to determine, these appendages are absolutely peculiar to this sub-family. On this basis I feel inclined to exclude *Ph. anomalocoela* Haswell 1905 from the sub-family Phaenocorinae until such time it may be determined whether it possesses such appendages or not.

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Description of New Species.

Phaenocora virginiana: Length in extended condition from 0.7 to 1.3 mm; width, about $^1/_5$ length of body; pharynx, robust, usually with ring of pigment surrounding its base; anterior end of body rather broad but falls away gradually to form a rather long but blunt tail-papilla; eye pigment often congregated into bean-shaped accumulations but may form large irregularly-shaped masses; pigment often confined to eyes and pharynx but may be scattered in patches over entire body; "Stäbchenstrassen" extend from either side of pharynx to end af "snout"; dermal rhabdites present in great numbers; ventrally-placed yolk glands anastomose freely and extend from either side of the base of pharynx to posterior end of body but usually retain evidences of their originally paired condition; testes compact and lobulated and extend from base of pharynx to the posterior third of body; male copulatory organ of the simple sac-within-a-sac construction (Type I) and unarmed, about $^1/_{12}$ length of body in invaginated condition; female genital canal moderately long and of fairly even size throughout and irregularly covered by giant unicellular glands which gives it a warty appearance; ductus

genito-bursalis rather short and projects into bursa intestinalis formig a valvular structure; bursa intestinalis usually a simple sac which opens into the enteron by means of a porus; common yolk- and oviduct enters at junction of female genital canal and ductus genito-bursalis; unicellular glands which enter female genital canal are of a simple type, the ducts of which enter the canal singly and not in clumps or sheaves as in *kepneri* and *highlandense*; usually colored a very dark green by means of numerous zoochlorellae.

Phaenocora kepneri: Length in extended condition 2 to 2.5 mm; width about $^1/_5$ the length of the body but appears much more slender than *virginiana* as it is much narrower anteriorly in the region of pharynx; pharynx slender with no pigment-ring associated with base; posterior end of body falls away rapidly ending in a short, sharp tail-papilla; eye-pigmentation irregular but most of the pigment confined to neighborhood of the eyes and never scattered over surface of body, although a few granules have been found on surface of pharynx at times; "Stäbchenstrassen" as in *virginiana;* dermal rhabdites are present as in *virginiana;* ventrally-placed yolk glands as in *virginiana* but apparently of finer texture and their double origin usually not quite so evident; testes follicular in structure and extend from slightly behind base of pharynx nearly to the posterior end of body; male copulatory organ (Type II) divided by a muscular diaphragm into a proximal portion containing the sperm and granular secretions and a distal portion housing an extremely long ductus ejaculatorius; the latter lined with an extremely heavy, regularly folded cuticula; distal end of ductus ejaculatorius when evaginated thrown into lobes which are armed with thorns of two sizes (3 μ and 1.5 μ respectively); length of male copulatory organ relatively enormous, being about $^1/_7$ the length of the fully extended individual; a well-marked male genital canal present; female genital canal very long and tapers gradually from atrium to its proximal end; giant unicellular gland-cells not distributed over surface of female genital canal as in *virginiana* but 5 enormous, spherical unicellular gland-cells are typically found at the junction of female genital canal and ductus genito-bursalis; ductus genito-bursalis moderately long; bursa intestinalis usually very large and thrown into numerous folds and prominences; ductus bursa-intestinalis long and its proximal end where it enters enteron guarded by a definite valvular apparatus; the long female genital canal, the moderately long ductus genito-bursalis, and the extremely long ductus bursa-intestinalis allow great freedom of position of the bursa intestinalis so that it may often be found lateral to the posterior third of the pharynx; common yolk- and oviduct enters at junction of female genital canal and ductus genito-bursalis; pear-shaped unicellular glands which empty into female genital canal are highly developed and their ducts are aggregated into clumps or sheaves as they enter the canal and not singly as in *virginiana,* usually colored light green by zoochlorellae.

Phaenocora highlandense: Length in extended condition 3 to 3.7 mm; much more sturdy in appearance than either of the preceding species; posterior end of body broad and falls away rapidly ending in a short, blunt tail-papilla; pharynx robust; granular pigment confined to eyes in all specimens which I have studied; a rich red pigment (probably soluble in alcohol as it is not found in sections) colors the region from snout to base pharynx[1]; "Stäbchenstrassen" as in the two preceding species; a few scattered dermal rhabdites present in addition to mucous glands; yolk glands anastomose freely and bear dorsal extensions as described for *baltica;* testes tubular and ramify freely; male copulatory organ relatively small, being only about $^1/_{18}$ the length of the fully extended animal; sperm separated definitely from granular secretions by means of a diaphragm; penis *sensu stricto* retracted into space which contains dorsally the granular secretions (Type III); thorns confined to distal end of evaginated "penis"; no male genital canal; female genital canal short and thick; giant unicellular gland-cells of female genital canal wanting; no ductus genito-bursalis; bursa-intestinalis similar to that of *kepneri* but separated into two quite definite compartments—one dorsal and one ventral in position; ductus bursa-intestinalis moderately long and springs from dorsal compartment; proximal end of ductus guarded by valvular apparatus as in *kepneri;* common yolk- and oviduct enters female genital canal some distance from its proximal end; the pear-shaped unicellular glands which empty into the female genital canal are as in *kepneri* with their ducts aggregated into sheaves; color opaquely white to highly green due to zoochlorellae.

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General Considerations.

Observations on my three species and my review of the literature concerned leads me to believe that the possession of "eyes", in the sense of eye-pigment, is a character to which it is dangerous to assign phylogenetic and systematic significance as the possession of eye-pigment is an extremely variable character.

The pear-shaped appendages of the atrium can not be considered either rudimentary or vestigial uteri as they are quite highly developed in *polycirra,* which possesses two uteri, as in the rest of the phaenocoras. Their function may be to prevent self-fertilization and they also, in all probability, serve some part in cocoon-building.

The yolk and oviducts of my three species do not enter the female genital canal independently but form a common yolk- and oviduct.

A study of the male copulatory organs of my three species together with a review of the male organs of the other described phaenocoras, leade me to

[1] I have occasionally found the same region in *virginiana* and *kepneri* colored a delicate rose-color but never a deep red as in *highlandense.*

believe that they may be placed under three types which probably form a phylogenetic series.

A similar study of the female copulatory organs appears to reveal seven types.

The female copulatory organs are much more variable than the male; consequently, the male organs are much more reliable as systematic indices.

I have been unable to determine any satisfactory correlation between the type of male and female copulatory organs and between either the possession or absence of eyes or body form. This, however, may be due to incomplete or faulty descriptions on the part of some investigators who were more concerned with the shape, size, and number of the thorns which armed the penis than they were with fundamental structures.

The characters of *Phaenocora* (*Megaloderostoma*) *polycirra* as outlined by BEKLEMISCHEV (1929) do not appear to be sufficiently unique to justify BRESSLAU (1933) in placing this species in a new genus (*Megaloderostoma*).

ADDENDUM.

Since completing this paper, I have had the opportunity of reviewing a paper by BEKLEMISCHEV (1921) in which on pages 641 and 642 he gives interesting notes concerning *Ph. typhlops* Vejd. and *Ph. unipunctata* Örst.

Concerning *Ph. typhlops,* he points out that he found specimens of *typhlops* in which the armament of the penis resembled that of *Ph. vjatkensis* as described by NASONOV (1919). The number of rows of thorns varied from 5 to 8 and the greater the number of thorns, the more closely they approached being of uniform size.

The above facts confirm my contention that the "thorning" of the penis is a variable character. Furthermore, they support my views as to a doubt of the validity of *vjatkensis* as a species (see pp. 151—153).

With reference to *Ph. unipunctata,* among other less important things, he points out that he found in his larger specimens yolk glands with dorsal extensions as described by M. BRAUN (1885) for *baltica* (incidentally also by me for *highlandense*) and that these animals also showed differences in the form and extent of their testes as compared with the smaller individuals. He was quite sure they were of the same species, however, as their copulatory organs were identical with those of his smaller animals. Again we have what appear to be variable characters which, in this case, are probably due to differences in functional activity.

BEKLEMISCHEV finally describes and pictures (Plate II, figs. 12 and 13) the copulatory organs of his animals. As far as the female organs are con-

cerned, as described by BEKLEMISCHEV, they differ very little from the description and figure of BENDL (1909) with the exception that a bursa intestinalis is more evident in BENDL's figure (BEKLEMISCHEV states that the stalk of the "receptaculum" is very little differentiated in his animals) and that the ductus bursa-intestinalis is drawn as being very narrow in his figure, while in BENDL's figure a ductus bursa-intestinalis is hardly indicated at all —the bursa being so close to the enteron, that I have already indicated (p. 117), that the opening into the enteron might be by means of a porus rather than by a ductus. Furthermore, BEKLEMISCHEV does not describe a valvular apparatus guarding the entrance into the enteron, although he says that he determined the position of its entrance by means of sections.

With reference to the male organ, I am still in as great a quandary with reference to what the organ is actually like in this species as I was before reading his paper—every author seems to describe it differently. According to BEKLEMISCHEV's figure 13, drawn from the living animal, showing the organ in the resting condition, it is of a decidedly elongated egg-shape, noticeably compressed at its equator in a region where a partition, pierced at its center by a hole, divides the interior of the organ into two almost equal halves—the upper half containing the sperm, while the lower half contains the granular secretion. We could, therefore, say that there is a definite vesicula seminalis and granulorum. A very short ductus ejaculatorius is pictured as being invaginated into the space occupied by the granular secretions. In his figure 12 he shows the ductus ejaculatorius in its evaginated condition. Now, I can not imagine how this "penis" could ever be long enough to ever extend through the genital pore, much less being able to enter the genital pore of a co-copulant. Furthermore, I can see no mechanism by which it could be evaginated except by a pressure of the granular secretion during compression and if once evaginated, I do not see how it could be invaginated again. Unfortunately, BEKLEMISCHEV does not give us any description of the histology of the organ, although he must have sections of the animal, as he mentions sections with reference to the determination of the position of the ductus bursa intestinalis. He tells us nothing of the character of the partition, the structure of the walls, nor of the presence or absence of a "Plasmamasse". He does say, however, that the male organ is more like that of a *Bothromesostoma* than a *Phaenocora*. However, I feel that with further investigation its phaenocora-like characters may be determined.

In his figure 13 he shows the pear-shaped appendages of the atrium relatively in their proper position but does not show their division into internal and external lobes. Nor, as far as my experience goes, do I believe their inner ends should be so closely approximated. As a matter of fact, I would expect to see the inner lobes almost entirely retracted from the atrium with the penis in the resting condition.

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LEGEND.

ab. Anterior branch of protonephridium.
am. Male genital atrium.
agc. Giant atrial gland cell.
agc$_1$. Another type of atrial gland cell.
agc$_2$. Still another type of atrial gland cells.
am. Muscular strands which loosely attach inner sac of male copulatory organ of *Ph. virginiana* to the outer sac of the same. Note that in fig. 44, *am* represents such a strand and not a complete diaphragm.
ba. Cirruli of male copulatory organ of *Ph.* (*Megaloderostoma*) *polycirra.*
bm. Basement membrane of atrium.
bm$_1$. Basement membrane of epithelium of body.
bi. Bursa intestinalis.
cd. Common yolk- and ovi-duct.
cep. Cytoplasmic end-processes of the cells of ductus bursa-intestinalis.
cm. Circular muscles.
cm$_1$. External circular muscle layer of male copulatory organ.
cm$_2$. Inner circular muscle layer of male copulatory organ.
cmf. Circular muscle fibers.
co. Male copulatory organ.
cpm. Cytoplasmic processes of the muscles of female genital canal.
cu. Cuticular layer of ductus ejaculatorius in figs. 50, 52, 55.
cu$_1$. Cuticular layer of the bulbus and diaphragm of the male copulatory organ of *Ph. kepneri.*
cut. Cuticula.
cv. Commisural vessel of the protonephridia of *Ph. highlandense.*
dbi. Ductus bursa-intestinalis.
dc. Distally situated cells.
de. Ductus ejaculatorius (part which becomes evaginated).
de$_1$. Definitive ductus ejaculatorius (part which never becomes evaginated).
dgb. Ductus genito-bursalis.
dgi. Ductus genito-intestinalis.
dgl$_1$. Lumina of ducts of unicellular glands (*gl*$_4$) which empty into female genital canal.
di. Diaphragm of male copulatory organ of *Ph. kepneri.*
di$_1$. Diaphragm bounding proximal portion of penis *sensu stricto* of *Ph. highlandense.*
di$_2$. Diaphragm separating vesicula seminalis from granulorum in *Ph. highlandense.*
di$_a$. External diaphragm of the male copulatory organ of *Ph.* (*Megaloderostoma*) *polycirra.*
di$_b$. Internal diaphragm of the male copulatory organ of *Ph.* (*Megaloderostoma*) *polycirra.*
dm. Dilator muscles. (In fig. 27.)
dm. Outer diagonal layer of muscles of male copulatory organ.
dm$_1$. Inner diagonal layer of muscles of male copulatory organ.
e. Eyes.
ec. External cells of valvular apparatus of ductus bursa-intestinalis.
eg. Egg (cocoon).
en. Enteron.
ep. Excretory pores.
es. Egg (cocoon) shell.
fgc. Female genital canal.
fib. Fibrillar structure.
ga. Genital atrium.
gc$_1$. Giant gland cells situated at the junction of the female genital canal and the ductus genito-bursalis in *Ph. kepneri* and also somewhat similar cells of the female genital canal of *Ph. virginiana.*
gg. Glands which produce the granular secretion of the granulorum.
gl. Unicellular glands.
gl$_2$. Unicellular gland which empties into the common yolk- and ovi-duct.
gl$_3$. Second series of unicellular glands associated with the oviduct of *Ph. highlandense.*
gl$_4$. Unicellular glands emptying into the distal portion of the female genital canal.
gl$_5$. Group of large unicellular glands asso-

ciated with the male copulatory organ of *Ph. virginiana.*

gl$_6$. A similar group of unicellular glands associated with the male copulatory organ of the same species.

gl$_7$. Small unicellular glands associated with the male copulatory organ of *Ph. virginiana.*

gl$_8$. Large unicellular glands associated with the male copulatory organ of Ph. kepneri, probably homologous with *gl*$_5$ and *gl*$_6$ of *Ph. virginiana.*

glc. Group of glandular cells which are attached to the pear-shaped appendages of the atrium.

gp. Genital pore.

gs. Granular secretions of the granulorum.

ic. Internal cells of the valvular apparatus of the ductus bursa intestinalis.

icc. Intracellular cavities (Nebenhohlräume).

iga. Inferior genital atrium.

l. Lumen.

l$_1$. Distal lobe of the "penis" of *Ph. virginiana.*

l$_2$. Proximal lobes of the "penis" of *Ph. virginiana.*

lb. Lobe of gland (*gl*$_2$) in *Ph. virginiana.*

mf$_1$. Muscle fibers involving giant gland cells.

mgc. Male genital canal.

ms. Main stems of the protonephridia.

nu. Nucleus.

nu$_2$. Large nucleus at junction between female genital canal and bursa intestinalis of *Ph. highlandense* in fig. 16.

od. Oviduct.

ov. Ovary.

pb. Posterior branches of the protonephridia.

pbi. Porus bursa intestinalis.

pc. Proximally situated cells of the pear-shaped appendages.

pg. Pigment granules.

pg$_1$. Pigment ring at base of pharynx in *Ph. virginiana.*

ph. Pharynx.

pl. Lobes of the "Plasmamasse".

pm. "Plasmamasse".

pmu$_1$. Protractor muscles of the male-copulatory organ.

pmu$_2$. Protractor muscles of the pear-shaped appendages of the genital atrium.

pn. Protonephridium.

psa. Pear-shaped appendages of the genital atrium.

psa$_1$. Portion of the pear-shaped appendages which is never included within the genital atrium.

psa$_2$. Portion of the pear-shaped appendages which may be protruded into the genital atrium.

rmu. Retractor muscles of the pear-shaped appendages of genital atrium.

rs. Stäbchenstrassen.

s. Granules of the secretion of unicellular glands (*gl*$_4$) which stain red with MALLORY's after ZENKER's fluid.

sc. Secretory cell.

sc$_1$. Cavity containing sperms and granular secretions.

sg. Shell glands.

sga. Superior genital atrium.

sm. Strands of the granular secretions which stain blue with MALLORY's after ZENKER's fluid in figs. 51 and 63.

sm. Sphincter muscles.

sp. Sperm.

ss. Substance which forms shell of cocoon.

t. Thorns or denticles which arm the ductus ejaculatorius.

tc. Testes.

tgl$_4$. Transverse section of glands (*gl*$_4$).

ts. Sac-like portion of the ductus ejaculatorius of *Ph. kepneri* which is lined with thorns.

vac. Vacuole.

vc. Cells which form valve of porus bursa intestinalis in *Ph. virginiana.*

vd. Vas deferens.

vg. Vesicula granulorum. Only a definite granulorum in *Ph. highlandense* where the granular secretions are separated from the sperms by a diaphragm.

vs. Vesicula seminalis. Only a true vesicula seminalis in *Ph. highlandense.*

x. Area where evagination of ductus ejaculatorius commences.

yg. Yolk glands.

yd. Common yolk duct.

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EXPLANATION OF FIGURES.

PLATE I.

Fig. 1. *Ph. virginiana.* Ventral aspect of living animal. (x 83.)

Fig. 2. Figure showing changes in the shape of *Ph. virginiana.*

Fig. 3. 4. 5. Camera lucida drawings from total mounts of *Ph. virginiana* illustrating variations in pigmentation. Pigment ring (pg_1) at base of pharynx quite typical but not constant. (x 76.)

Fig. 6. *Ph. kepneri.* Ventral aspect of living animal. (x 50.)

Fig. 7, 8. Camera lucida drawings from total mounts of the anterior portion of *Ph. kepneri* showing variations in pigmentation of the "eyes". (x 76.)

Fig. 9. *Ph. highlandense.* Ventral aspect of living animal. (x 40.)

Fig. 10. Sagittal section through female copulatory organs of *Ph. virginiana.* Beauchamp's fluid; Mallory's. (x 374.)

Fig. 11. Transverse section through ovary, female genital canal, and superior genital atrium of *Ph. virginiana.* Note large glandular cells (gc_1) associated with female genital canal. Goldschmidt's fluid. Delafield's haematoxylin and eosin. (x 467.)

Fig. 12. Longitudinal section through ovary, female genital canal and portion of superior genital atrium of *Ph. kepneri.* Note degenerated condition of the epithelium which lines female genital canal (*fgc*) and the giant gland cells (gc_1) limited to the proximal end of the female genital canal. Drawn to the same scale as fig. 10. Beauchamp's fluid. Mallory's. (x 374.)

Fig. 13. An almost longitudinal section through the female genital canal of *Ph. kepneri* showing degenerating epithelium with the fibrillae (*fib*) with their ends twisted into paint-brush-like points. Beauchamp's fluid. Mallory's. (x 374.)

PLATE II.

Fig. 14. Sagittal section through pharynx, ductus bursa-intestinalis and portion of female genital canal of *Ph. kepneri.* Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 15. Sagittal section through pharynx, bursa intestinalis, a portion of ductus genito-bursalis, and proximal end of female genital canal of *Ph. kepneri.* A very small portion of the ductus bursa-intestinalis is also shown in this figure. From the same series of sections as fig. 14. (x 374.)

Fig. 16. Nearly sagittal section through pharynx, bursa intestinalis, female genital canal, and superior and inferior genital atria of *Ph. highlandense.* Note that this figure is drawn to the same scale as figs. 10, 12, 14, and 15. Beauchamp's fluid. Mallory's. (x 374.)

Fig. 17. Section through the porus bursa-intestinalis of *Ph. virginiana.* Goldschmidt's fluid. Delafields haematoxylin and eosin. (x 467.)

Fig. 18. Section through proximal end of female genital canal of *Ph. virginiana,* and portions of ductus genito-bursalis and bursa intestinalis. Note fibrillar structure of the degenerated epithelium of the female genital canal and the sperms which are escaping into the enteron. Goldschmidt's fluid. Mallory's. (x 467.)

Fig. 19. Section through bursa intestinalis of *Ph. kepneri* showing the many irregularly arranged muscle fibers which are responsible for its lobulated conditions. Also note muscle fibers which apparently constrict the giant gland cell(gc_1) of the

proximal end of the female genital canal and furthermore note the fibrillar structure (*fib*) of its cytoplasm and the granular secretion within its lumen. Beauchamp's fluid. Mallory's. (x 374.)

Fig. 20. Section through ductus bursa-intestinalis of *Ph. kepneri* near its point of entrance into the enteron. Note sperms (*sp*) contained in vacuoles within the epithelial cells of enteron. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 21. Section through the valvular apparatus of *Ph. kepneri* showing the discharge of sperms into the enteron. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 22. A section directly through the porus bursa-intestinalis of *Ph. virginiana* showing character of cells guarding its entrance. From same series of sections as fig. 18. (x 467.)

Fig. 23. Another section through valvular apparatus of ductus bursa-intestinalis of *Ph. kepneri*. Apparatus nearly closed, but with sperms escaping into enteron. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 24. Longitudinal section through the bursa intestinalis and porus of *Ph. virginiana*, showing petal-like arrangement of cells and the sperm being discharged into enteron. Goldschmidt's fluid. Mallory's. (x 467.)

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PLATE III.

Fig. 25. Section through the ductus bursa-intestinalis of *Ph. highlandense* and its valvular apparatus. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 530.)

Fig. 26. Section through the valvular apparatus of the ductus bursa-intestinalis of *Ph. highlandense*, showing the external cells (*ec*) sheathing the cytoplasmic end processes of the cells of ductus proper. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 530.)

Fig. 27. Section through part of bursa intestinalis and three of the giant cells (gc_1) at the proximal end of the female genital canal, showing the entrance of the common yolk- and ovi-duct (*cd*). Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 28. Section through the ovary of *Ph. kepneri*, showing the relationships of the oviduct (*od*), common yolk duct (*yd*), gland (gl_2), and common yolk- and oviduct. Bauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 29. Longitudinal section through the valvular apparatus of the ductus bursa-intestinalis of *Ph. highlandense*. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 467.)

Fig. 30. Another section slightly below the above from the same series of sections. (x 467.)

Fig. 31. B. A sagittal section through the anterior-ventral part of *Ph. kepneri*, showing the great extent of the glands associated with the female genital canal, the granular portion of the secretion of which stain a bright red with Mallory's. (x 234.) A. A greatly enlarged section showing the opening of some of these glands into the female genital canal. (x 1120.) Hot Zenker's fluid. Mallory's.

Fig. 32. Section through the female genital canal of *Ph. kepneri*, showing entrance of shell glands. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 33. An almost transverse section through the ductus bursa intestinalis of *Ph. highlandense*. Beauchamp's fluid. Mallory's. (x 467.)

Fig. 34. An almost longitudinal section through the female genital canal of *Ph. highlandense* in which no degeneration of the lining epithelium is evident. Note nuclei end cell-boundries of cells and fibrillar structure of cytoplasm. Compare with fig. 18. Beauchamp's fluid. Mallory's. (x 374.)

Fig. 35. Section through female genital canal and ovary of *Ph. virginiana*, showing lobular extensions (*lb*) of gland (gl_2) into the mouth of the oviduct. Goldschmidt's fluid. Mallory's. (x 374.)

Fig. 36. A somewhat similar section from a slide of *Ph. kepneri*. No lobes are evident, but the dark-staining secretion is extremely so. A series of sections reveals that the gland (gl_2) is actually about three times as large as shown. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 37, 38. Two sections from a series of *Ph. virginiana*, showing oviduct, common yolk duct, gland, etc. Goldschmidt's fluid. Delafield's haematoxylin and eosin. (x 467.)

PLATE IV.

Fig. 39. Longitudinal section through superior genital atrium and part of male copulatory organ of *Ph. kepneri*. (*agc*), giant gland cells of the superior genital atrium. (agc_1), other gland cells associated with atrium. Beauchamp's fluid. Mallory's. (x 234.)

Fig. 40. Transverse section through the "penis" and the interior lobes (psa_2) of the pear-shaped appendages of *Ph. virginiana*. Note that the evaginated "penis" is almost completely surrounded by the plastic lobes. The yolk glands (*yg*) are enormously developed in this specimen. Zenker's fluid. Mallory's. (x 374.)

Fig. 41. Male and female copulatory organs of *Ph. virginiana*. A camera lucida drawing from a total mount. Zenker's fluid. Borax carmine. (x 374.)

Fig. 42, 43. Two sections through one of the pear-shaped appendages of the genital atrium of a gravid *Ph. virginiana*. Note that the proximal lobe of the appendage has been completely withdrawn from the atrium and that its proximal cells (*pc*) are in a state of degeneration while its distal cells are still intact. Goldschmidt's fluid. Delafield's haematoxylin and eosin. (x 187.)

Fig. 44. A. Section through the un-evaginated male copulatory organ and genital atrium of *Ph. virginiana*. Note that it does not possess a "permanent penis". The fibers (*am*)—see also fig. 58—loosely attaches the inner sac to the outer. There is no diaphragm as in *kepneri*, but the condition in *kepneri* was probably brought about through a complete fusion of the proximal parts of both sacs. (x 187.) B. A greatly enlarged drawing of the external lobe of the pear-shaped appendage, two sections removed from (psa_1) in A. (x 561.) Goldschmidt's fluid. Delafield's haematoxylin and eosin.

Fig. 45. Longitudinal section through the evaginated male copulatory organ of *Ph. virginiana*, showing that the inner lobes (psa_2) of the pear-shaped appendages have met dorsally and have occluded the passage into the female genital canal. Zenker's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 46, 47, 48, 49. A series of transverse sections through the genital atria and pear-shaped appendages and portion of male copulatory organ of *Ph. kepneri*. Note that in this case in which the male organ is not evaginated that a major part of the inner lobes has been withdrawn from the atrium. Note the giant glandular cell (*agc*) in fig. 47. The nuclei of the cells of the atrium are quite evident in these figures which the degeneration of the epithelium is quite evident. Beauchamp's fluid. Mallory's. (x 374.)

PLATE V.

Fig. 50. Almost sagittal section through the male copulatory organ of *Ph. kepneri.* Note pleated condition of cuticula (*cu*) which lines the ductus ejaculatorius and the powerful longitudinal (*lm*) and the weak circular (*cm*) associated with the same. Sublimate. Mallory's. (x 186.)

Fig. 51. Section through the male copulatory organ, male genital canal, superior and inferior genital atrium, and genital pore of *Ph. kepneri.* Note that the part of the ductus which is capable of evagination (*de*) is greatly coiled in this specimen. Definitive ductus ejaculatorius (de_1), Zenker's fluid. Mallory's. (x 186.)

Fig. 52. Enlarged section of the ductus ejaculatorius of *Ph. kepneri* taken from same series of slides as fig. 51. (*nu*) nuclei of degenerating epithelium. (x 747.)

Fig. 53. Camera lucida drawing of the male copulatory organ of *Ph. kepneri.* Drawn from living animal under pressure of cover-glass. (x 187.)

Fig. 54. Camera lucida drawing of the male copulatory organ of *Ph. kepneri,* in the evaginated condition. (x 118.)

Fig. 55. Section through the partially evaginated ejaculatorius of *Ph. kepneri.* Note how the cuticula of the ductus ejaculatorius has become closely folded in the portion which has not as yet become evaginated. Beauchamp's fluid. Delafield's haematoxylin and eosin. (x 374.)

Fig. 56. Distal end of the male copulatory organ of *Ph. highlandense.* Note diaphragm (di_2) separating penis *sensu stricto* from the cavity beneath the granulorum. Contraction of fixation has thrust end of penis into inferior genital atrium. Note highly contracted muscles (*mu*). Beauchamp's fluid. Mallory's. (x 187.)

Fig. 57. Section through male copulatory organ of *Ph. highlandense.* Note diaphragm (di_2) forming proximal boundry of penis *sensu stricto* and separating it from the cavity under granular glands. Note entrance of granular glands (*gg*) and vasa deferentia (*vd*). Beauchamp's fluid. Mollory's. (x 186.)

Fig. 58, 59. Two transverse sections through the proximal end of the male copulatory organ of *Ph. virginiana* showing the sac-within-a-sac construction. Note fibers (*am*) loosely attaching inner sac to outer sac. Beauchamp's fluid. Mallory's. (x 374.)

Fig. 60. Camera lucida drawing from total mount of the male copulatory organ of *Ph. virginiana.* Partially evaginated condition. Note lobes at distal end of "penis". (x 374.)

Fig. 61. Free-hand drawing of the male copulatory organ of *Ph. highlandense* from life. Notice the fully invaginated condition of the ductus ejaculatorius and diaphragm (di_1) separating vesicula seminalis from vesicula granulorum. (about x 260.)

Fig. 62. Free-hand drawing of the male copulatory organ of *Ph. highlandense* in the partially evaginated condition. (about x 200.)

Fig. 63. Transverse section through the bulbus of *Ph. kepneri.* Beauchamp's fluid. Mallory's. (x 186.)

Fig. 64. Section through the proximal part of the male copulatory organ of *Ph. highlandense.* Note diaphragm (di_1) separating vesicula seminalis from granulorum and diaphragm (di_2) separating penis *sensu stricto* from space under granulorum. Beauchamp's fluid. Mallory's. (x 186.)

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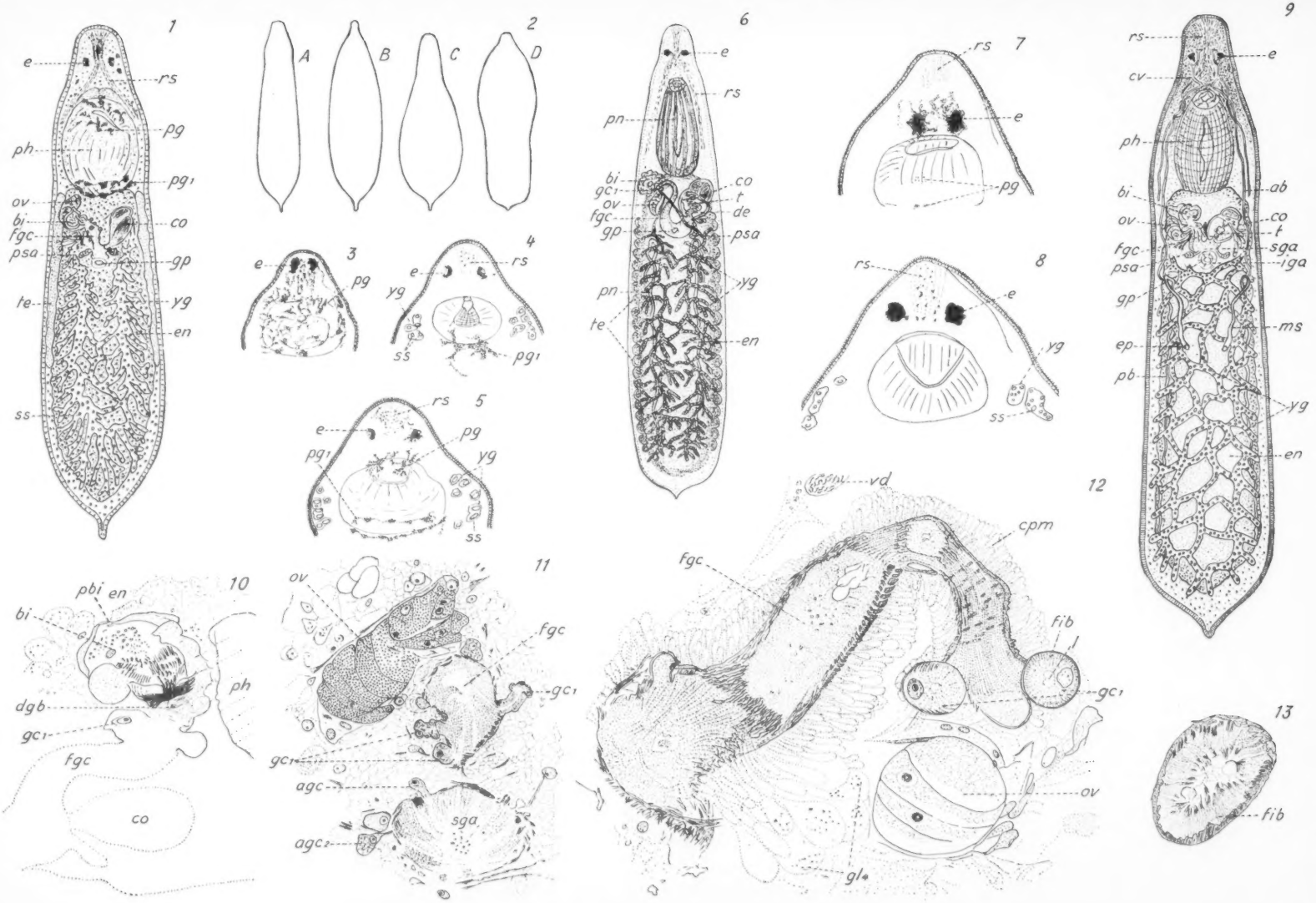
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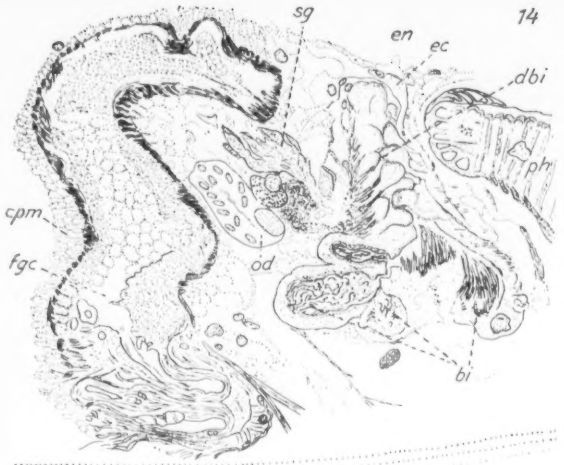

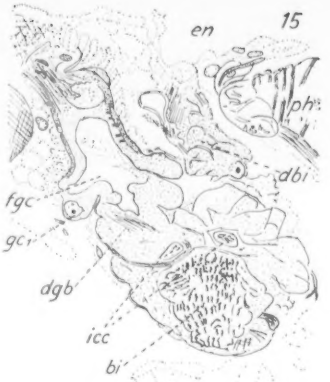

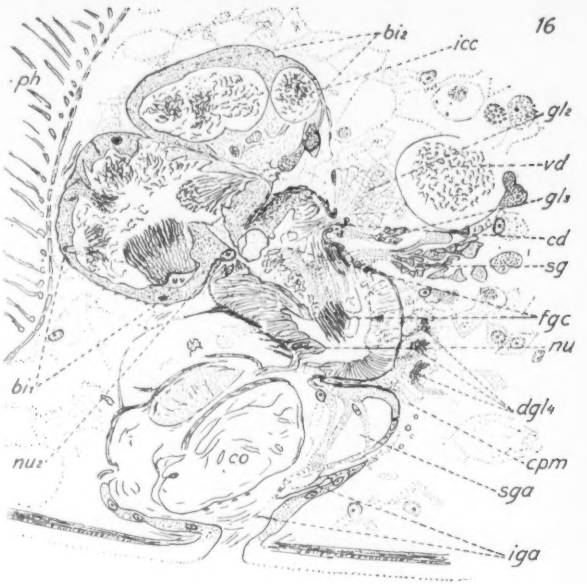

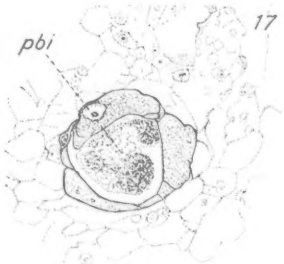

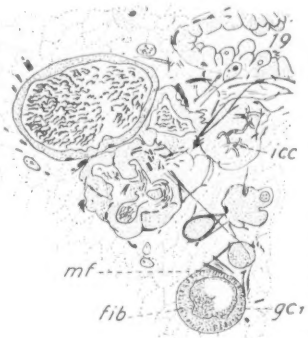

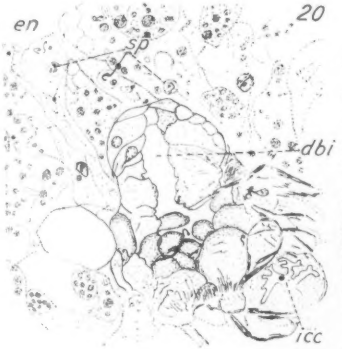

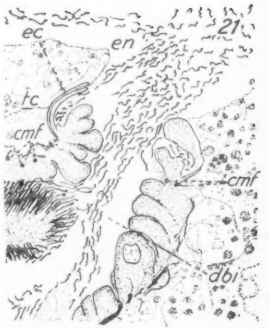

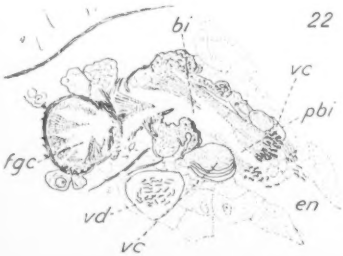

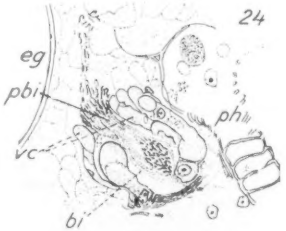

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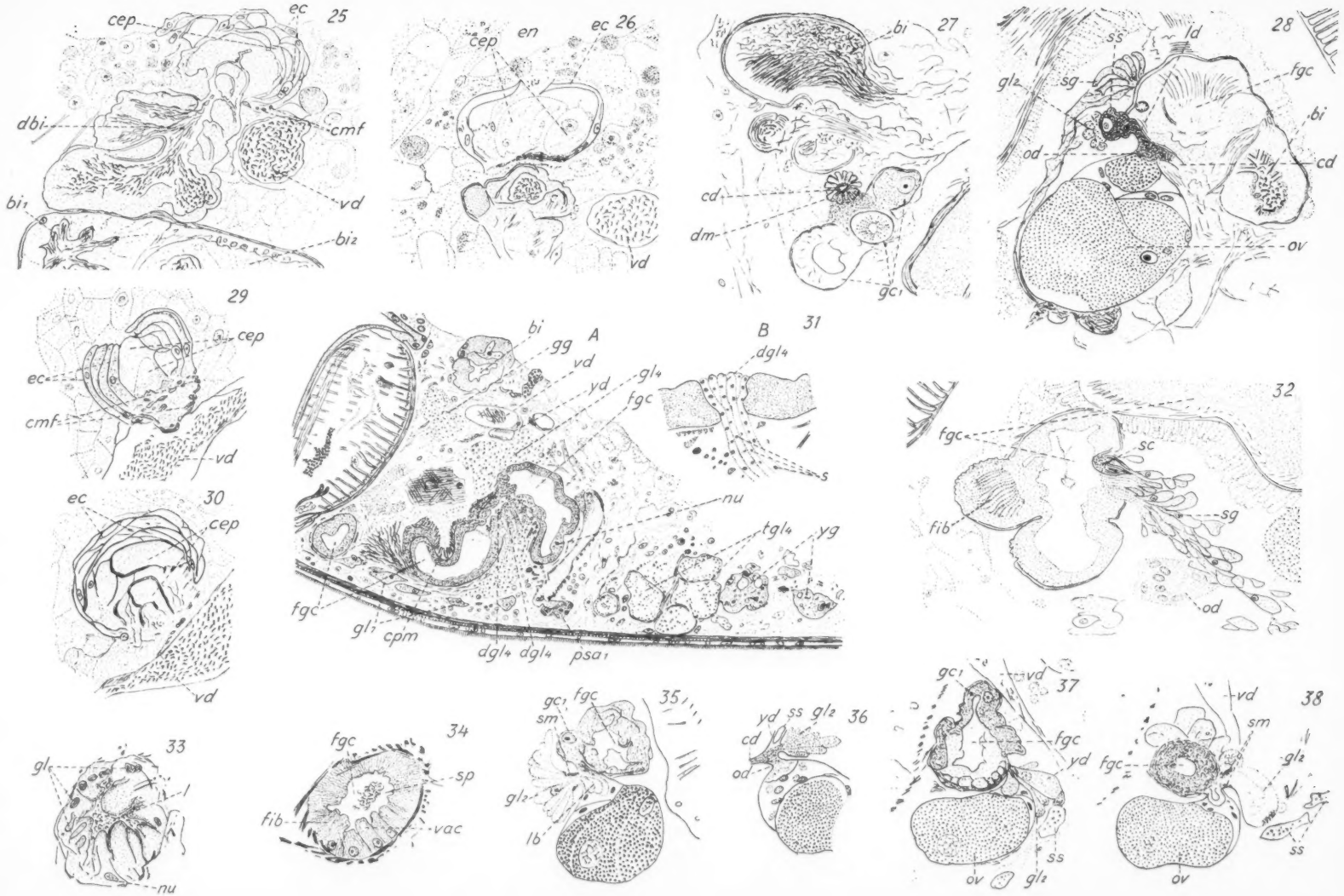
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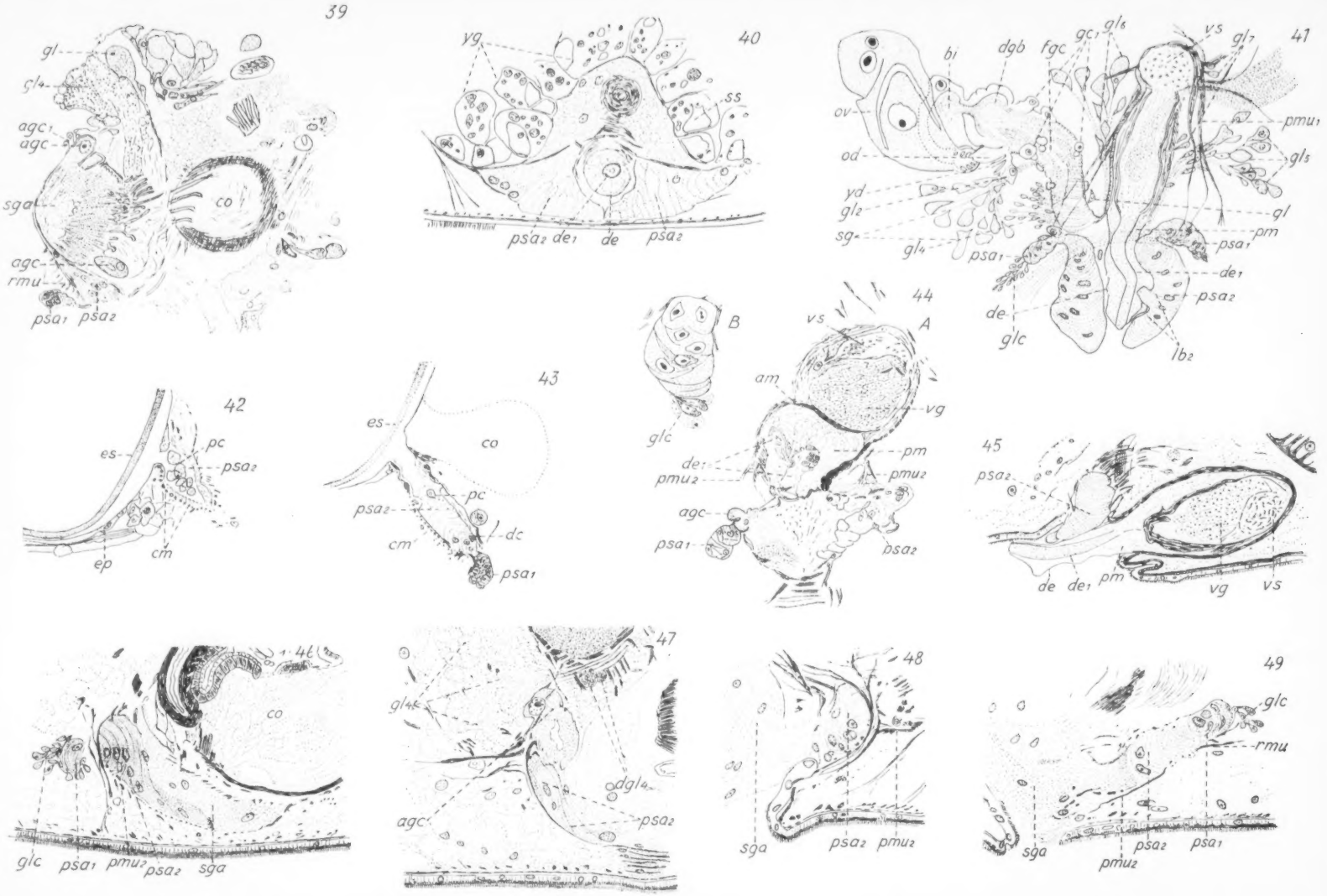

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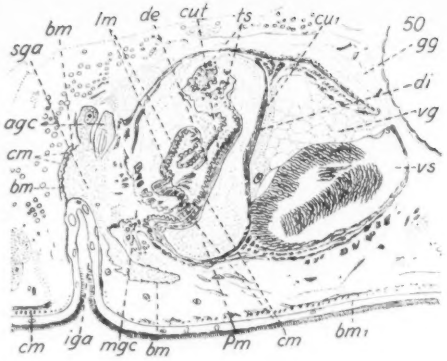
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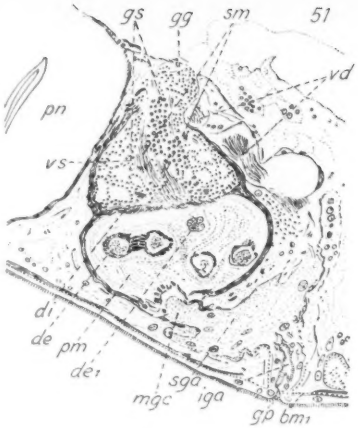
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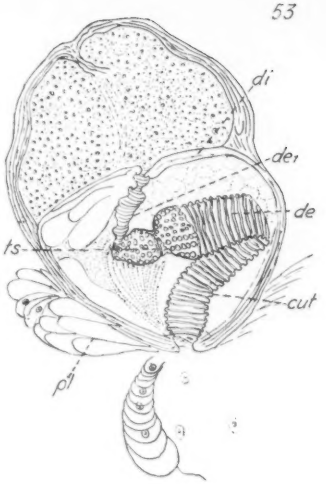
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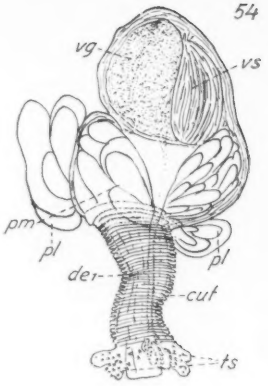
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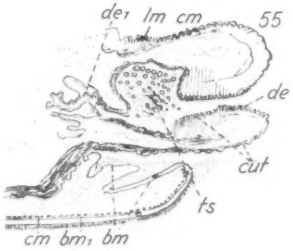
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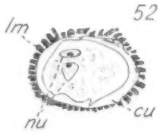
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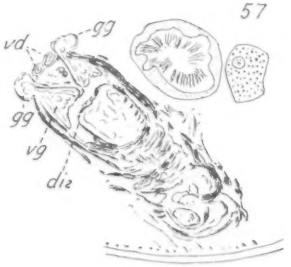
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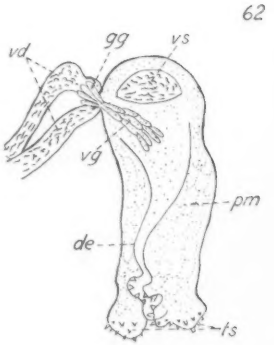
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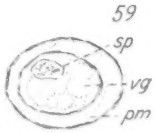
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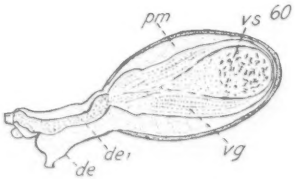
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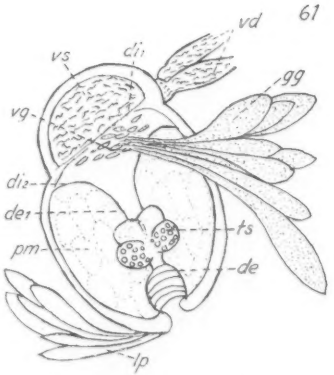
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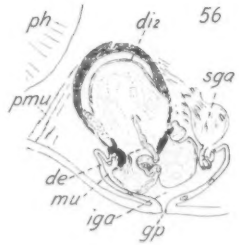
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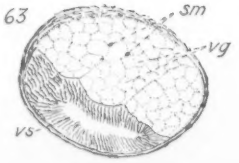
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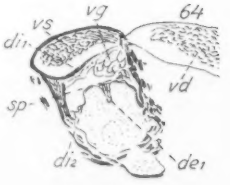
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PLATE V.

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ABWEICHUNGEN VON DER ELTERNFORMEN IN DER EMBRYONALEN ENTWICKLUNG DER BASTARDE VON COREGONUS BAERI KESSL. × SALMO FARIO LAC. L.

VON

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(Aus Laboratorium für allgemeine Biologie am 2. Leningrader Medizinischen Institut)

1. BASTARDIERUNG BEI FISCHEN.

Experimentelle Bastardierung ist mit Fischen verschiedentlich von vielen Forschern vorgenommen worden. Die erste uns bekannte Arbeit FISCHERS (1880) beschreibt die Bastarde zwischen Karpfen (Cyprinus carpio) und Karausche (Carassius auratus). Etwas später führte APPELLÖF (1894) Kreuzungen zwischen entfernteren Arten aus (Gadus morrhua × Gasterosteus aculeatus), doch schliesst seine Beschreibung mit dem Furchungsstadium. Von 1904 an beschäftigte sich eine Reihe von Forschern mit Kreuzungsversuchen zwischen verschiedenen Arten, hauptsächlich Seefischen, indem einige von ihnen (HERTWIG, G. u. P., 1914, MORRIS, 1914, MOENKHAUS, 1904, 1908, 1910, NEWMAN, 1906, 1910, 1915, 1918) Vertreter verschiedener Gattungen und sogar Familien mit einander kreuzten. In den letzten Jahren wurde eine noch nicht veröffentlichte Arbeit über die Kreuzung von Abramis brama und Carassius carassius ausgeführt (KRZYZANOWSKI), deren SEREBROWSKI (1935) in seiner Übersicht der Bastardierung erwähnt, und die Untersuchung von PROKOFJEWA (1934) über die Bastarde zwischen Coregonus Baeri und Salvelinus fontinalis. Sämtliche genannte Autoren verweilten in ihren Untersuchungen der Bastarde hauptsächlich bei Fragen der Genetik und schenkten ihre Aufmerksamkeit dem gegenseitigen Verhältnis zwischen den Chromosomen der elterlichen Geschlechtszellen, dem Charakter der Vorgänge in den Zellen, dem Tempo der Entwicklung und den Endstadien. Nur MOENKHAUS gibt eine kurze Beschreibung des inneren

Baues der Embryonen, ohne jedoch die mikroskopische Analyse anzuführen, obgleich er erwähnt, dieselben zum Teil an Schnittpräparaten untersucht zu haben.

In Bezug auf Bastarde weitläufig verwandelten Formen sind für die vorliegende Arbeit einige Angaben von MOENKHAUS, HERTWIG und PROKOFJEWA von Interesse (eingehendere Übersichten finden sich bei MORGAN und SEREBROWSKI); somit die Untersuchungen OPPERMANNS über Befruchtung der Forelle durch radiumbestrahlte Spermatozoen und diejenigen von TRIFONOWA über Parthenogenese bei Fischen.

G. u. P. HERTWIG haben verschiedene Bastarde von Seefischen zum Zwecke der Aufklärung des gegenseitigen Verhältnisses zwischen den elterlichen Chromosomen, sowie des Verlaufs der Zellteilung bei den Bastarden untersucht. In Fällen von Kreuzungen zwischen fernstehenden Arten (Gobius jozo × Crenilabrus pavo, Crenilabrus pavo × Box Boops) vermerken sie verschiedene Defekte in den karyokinetischen Figuren und in der Teilung des Protoplasmas der Blastomeren. Sie beschreiben Fälle fehlender Zellteilung und unvollständiger Teilung. In diesen Unregelmässigkeiten sehen sie die Ursache des Misserfolgs der Bastardierung, die darin zum Ausdruck kam, dass die erhaltenen Embryonen missgestaltete Formen besassen und in der Regel im Vergleich zur Kontrolle stark verkürzt waren.

Die von G. u. P. HERTWIG an den Bastarden beobachteten Unregelmässigkeiten in den Zellteilung gewinnen ein besonderes Interesse in Zusammenhang mit denen späteren PINNEYS (1918, 1928), OPPERMANNS (1923) und TRIFONOWAS (1930, 1935). Bereits früher wurde von LOEB der Gedanke ausgesprochen, dass man es bei Kreuzungen zwischen Fischen offenbar mit Parthenogenese zu tun hat, wie dieses in Bezug auf Kreuzungen zwischen vielen Echinodermata bekannt ist. PINNEY studierte die Chromosomen der Fischbastarde und beschreibt die Elimination derselben in Fällen von entfernten Kreuzungen, während bei der Bastardierung nahestehender Arten die Zellteilungen normal verlaufen. Unregelmässigkeiten in den Zellprozessen wurden auch von OPPERMANN beobachtet, der Forelleneier mit radiumbestrahlten Spermatozoiden befruchtete, also in Fällen künstlicher Parthenogenese. TRIFONOWA beschreibt in ihren Arbeiten (1930, 1935) von ihr untersuchte Fälle unzweifelhafter Parthenogenese bei einigen Süsswasserfischen (Acerina cernua, Abramis brama, Rutilus rutilus und Perca fluviatilis). Ihre Versuche stellten gleichfalls verschiedene Unregelmässigkeiten in den Zellvorgängen während der Furchungsperiode fest, als deren Folge Embryonen von missgestalteter Form entstehen. Die erhaltenen Embryonen besassen natürlich kleinere Ausmasse, als diejenigen der Kontrolle, und in einigen Fällen wurden an Chromatin ärmere Kerne beobachtet, wie die Verfasserin meint, eine Folge ihrer Haploidie. Diese Untersuchungen stellen unbedingt die Bastardnatur der früher beschriebenen Bastarde zwischen entfernt verwandten Arten

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in Frage, insofern bei der Mehrzahl der Beobachtungen (MOENKHAUS) die Zellprozesse nicht eingehend genug untersucht worden sind. In den uns am meisten interessierenden Arbeiten ist die Frage, ob Bastardierung oder Parthenogenese vorliegt, ungenügend beleuchtet.

Bei Besprechung der Bastarde Fundulus heteroclitus × Menidia notata und Fundulus heteroclitus × Gasterosteus bispinosus vermerkt MOENKHAUS nur die häufig vorkommende Dispermie und den im Vergleich zur Kontrolle verlangsamten Furchungsprozess. Das Absterben der von ihm untersuchten Embryonen erfolgte bald nach dem Beginn der Gastrulation, nachdem sich der Embryo formiert und die Zunahme des Gehirns und der Augenblasen eingesetzt hatte. Nur bei einigen Exemplaren schritt die Entwicklung etwas weiter fort. PROKOFJEWA macht wertvolle Angaben über die Anzahl der Chromosomen bei Coregonus Baeri, Salmo trutta und Salvelinus und Bastarden Coregonus × S. trutta und Coregonus × Salvelinus fontinalis. Die gefundene Anzahl der Chromosomen gestattet die Schlossfolgerung, dass bei den von ihr untersuchten Bastarden eine Befruchtung unzweifelhaft stattgefunden hatte.

2. MATERIAL UND METHODIK.

Wir haben uns die Aufgabe gestellt, an die Aufklärung des Embryonalprozesses bei Fischbastarden heranzutreten und die Ursachen der Einstellung der Weiterentwicklung und des Auftretens missgestalteter Formen festzustellen. Als Untersuchungsobjekt wählten wir mit dem Sperma von Salmo fario lac. L., Salmo salar L. und Salvelinus fontinalis lac. L. befruchtete eier von Coregonus lavaretus Baeri KESSL. Sämtliche Arten gehören derselben Familie der Salmoniden an. Salmo fario, Salmo salar und Salvelinus fontinalis sind einander nahestehende Arten der Gattung Salmo, während Coregonus lav. Baeri zu einer anderen, Salmo sehr fernstehender Gattung gehört.

Die Anzahl der Chromosomen ist bei den von uns gekreuzten Arten sehr verschieden. Nach den Angaben von PROKOFJEWA (1934) bildet die diploide Chromosomenzahl bei Coregonus lavaretus 80, der Forelle 84, Lachs 60 und bei Salvelinus fontinalis 80. Die Eier der Forelle, des Lachses und Salvelinus sind sehr gross und stimmen in der Grösse und Menge des Dotters überein. Der Durchmesser des Eies der Forelle beträgt ca. 6 mm, derjenige des Lachses 7—8 mm. Die Eier von Coregonus lavaretus sind bedeutend kleiner, ärmer an Dotter und der Durchmesser derselben erreicht nur 3 mm. In Zusammenhang mit dem Unterschied in der Dottermenge verläuft die Entwicklung der Embryonen bei der Forelle und dem Coregonus verschiedenartig. Bei der Forelle und dem Lachs breitet sich der Embryonalschild sehr langsam über den Dotter aus. Der Dotterpropfen schliesst sich spät, nachdem

der Embryo sich bereits formiert hat und gegen 30 Somiten besitzt. Dagegen übervächst der Embryonalschild bei Coregonus lavaretus schnell den Dotter und bedeckt ihn zur Zeit, wenn der Embryo sich zu formieren beginnt, vollständig. Die Eier von Coregonus lavaretus, Forelle, Lachs und Salvelinus werden im Spätherbst, Ende Oktober oder Anfang November, abgelegt, und ihre Entwicklung kommt im April zum Ausschlüpfen der Jungen. Die erste Furchungsperiode umfasst 4—6 Tage, in Abhängigkeit von der Temperatur des Wassers. Die ersten Anzeichen eines Embryos sind 1—2 Tage nach erfolgter Gastrulation wahrzunehmen. Der Embryo mit Anlage von Gehirnteilen, Augenblasen und den ersten Somiten entsteht 8—10 Tage nach der Befruchtung. Das langsame Entwicklungstempo gestattete uns die Verwendung von Material unter Verhältnissen, wie sie in der Züchterei herschen, wo sich die befruchteten Eier in Behältern mit fliessendem Wasser befinden.

Das Material für die vorliegende Arbeit wurde von der Neva-Fischzüchterei erhalten, wo die Eier von Coregonus lavaretus nach der üblichen Methode mit dem Sperma des Neva-Lachses, der Seeforelle und Salvelinus fontinalis befruchtet worden waren. Die Eier wurden in Petrunkewitsch' Flüssigkeit fixiert. Bei der weiteren Bearbeitung im Laboratorium wurden die Embryonen in toto unter dem Mikroskop (Obj. No. 1) betrachtet und darauf an Schnitten untersucht. In Stadien vor der Gastrulation wurden die Schnitte in zwei zu einander perpendikulär verlaufenden Richtungen ausgeführt. Spätere Stadien wurden hauptsächlich an 10—12 μ dicken Querschnitten studiert und nur einige Embryonen an Sagittalschnitten untersucht. Zur Färbung der frühen Stadien kam Hämatoxylin nach HEJDENHAIN und EHRLICH für Verwendung. Die Späteren Stadien wurden gleichfalls mit Hämatoxylin nach EHRLICH oder mit Boraxkarmin gefärbt. Alle Abbildungen wurden mit Hilfe des Zeichenapparates von totalen Objekten bei Obj. No. 1, Okular 2, an Schnitten bei Obj. No. 7, Okular 2, ausgeführt und nur einige Schnitte unter Immersion ($^1/_{12}$, Okular 10) gezeichnet.

Ich halte es für meine angenehme Pflicht meinem Lehrer Herrn Prof. Dr. P. P. Iwanoff meinen aufrichtigsten Dank auszusprechen.

3. DIE ERSTEN ENTWICKLUNGSSTADIEN DER BASTARDE.

Eine Entwicklung der Bastardeier liess sich schon nach 24 Stunden feststellen, als in allen Fällen 2 Blastomeren zu sehen waren. Alle Eier begannen sich zu entwickeln; folglich kann die Befruchtung als geglückt angesehen werden. Am dritten Tage bestand der Embryo aus 4—8 Blastomeren, am vierten aus 8—32; weiterhin ging die Teilung schneller vor sich. Die Form der Blastomeren und ihre Lage auf dem Dotter entsprach den Kontroll-

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stadien bei Coregonus lavaretus und glich im höchsten Grad den Furchungsbildern bei der Forelle. Ein bedeutender Unterschied zeigte sich nur im Tempo der Furchung, welches bei den Bastarden im Vergleich zur Kontrolle sehr verlangsamt war. Bei den Kontrollexemplaren von Coregonus lavaretus wurde das Stadium von 16—32 Blastomeren am 2. Tage beobachtet, und gegen Ende des 6. Tages erfolgte die Gastrulation. Ebenso machten die Forellenembryonen die Gastrulationsperiode am 4.—5. Tage durch. Indessen wurde bei den Bastarden die Bildung der peripherischen Verdickung des Embryonalschildes erst am 25. Tage wahrgenommen.

Die Betrachtung der Schnitte von Embryonen im Stadium von 8—16 Blastomeren und kurz vor der Gastrulation ergab dasselbe Bild, wie die Kontrolle. Die Zellteilung verlief normal. Die karyokinetischen Figuren zeigten keine Abweichungen. Wir haben an unseren Bastarden die von G. u. P. Hertwig und Pinney für eine Reihe von ihnen untersuchter Bastarde beschriebene unvollständige Teilung des Zellplasmas, doppelte Spindeln usw. nicht beobachten können. Wie Abb. 1, auf denen sagittale Schnitte durch die sich bildende Wölbung der Keimscheibe wiedergegeben sind, verlief auch dieser Vorgang bei den Bastarden und der Kontrolle gleichartig.

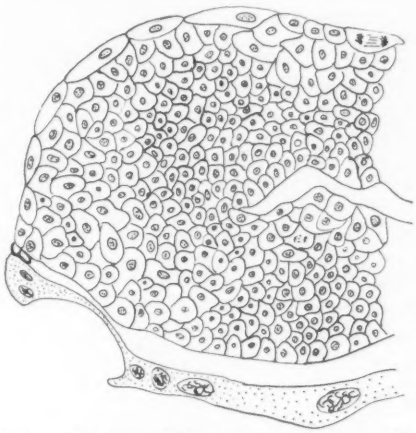

Abb. 1. Sagittalschnitt durch gastrulierende Teil des Embryonalschilds.

Bei der Untersuchung der Schnitte durch frühe Stadien, wurde selbstverständlich den Chromosomen Beachtung geschenkt, mit der Absicht festzustellen, ob nicht die Entwicklung das Resultat künstlich hervorgerufener Parthenogenese bildet, da gemäss den Angaben von Trifonowa (1930, 1935) parthenogenetische Entwicklung der Eier bei Fischen oft beobachtet wird. Von den Angaben über die Chromosomenzahlen bei den elterlichen Formen ausgehend, machten wir den Versuch die Chromosomen zu den Zellen der Bastarde zu zählen. Leider gibt die Fixationsflüssigkeit Petrunkewitsch' kein genügend deutliches chromosomale Bild, infolgedessen erwies sich eine genaue Zählung als unausführbar. Trotzdem konnte völlig sicher festgestellt werden, dass die Anzahl der Chromosomen bei den Bastarden Coregonus lavaretus $\times$ Salmo fario lac. bedeutend grösser ist als 40 (die haploide Chromosomenzahl bei Coregonus). Wir konnten deren gegen 50 zählen, wobei viele Chromosomen ungezählt blieben. Schon dieses allein spricht dafür, dass die Entwicklung der Embryonen infolge der Befruchtung stattgefunden

hatte. Dasselbe lässt sich von den Bastarden Coregonus Baeri × Salvelinus font. behaupten, bei denen die Anzahl der Chromosomen, nach Zählungen von PROKOFJEWA, 80 beträgt. Ebenso deutet das normale Bild der Karyokinese darauf hin, dass eine Vereinigung der Chromosomen des Eies mit denjenigen des Spermatozoiden stattgefunden hatte. Indem wir jedoch die Möglichkeit der Elimination von Chromosomen im weiteren Verlauf Rechnung trugen, richteten wir unser Augenmerk auf die karyokinetischen Figuren der späteren Entwicklungsstadien. Die ganz gegen Ende der Furchung statthabenden Zellteilungen verliefen gleichfalls völlig normal und ein normales karyokinetisches Bild zeigten auch die embryonalen Gewebe. Somit hatten wir es unzweifelhaft nicht mit parthenogenetisch entwickelten Eiern von Coregonus, sondern mit Bastarden zu tun.

4. BASTARDE COREGONUS LAVARETUS BAERI × SALMO FARIO LAC.

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Während der Gastrulationsperiode verlief die Entwicklung der Embryonen bei allen Bastarden gleichartig. Am vierundzwanzigsten Tage trat für alle Bastarde die kritische Periode der Gastrulation ein, die für sämtliche, mit dem Sperma von Lachs und Salvelinus befruchteten Eiern sich als tödlich erwies. Einen glücklichen Verlauf nahm die erste Gastrulationsperiode nur bei den Bastarden von Coregonus × Salmo fario. Aber auch hier fand gleich anfangs ein grosser Ausfall statt. Die Weiterentwicklung dieser Bastarde dauerte nur 14 Tage, dabei war das Prozent des täglichen Ausfalls ein sehr bedeutendes. Während dieser 14 Tage verfügten wir über gegen 400 Eier, von denen fast dreiviertel zu Grunde gingen. Gegen 100 Eier lieferten ausgebildete Embryonen. Die Gastrulationsperiode selbst, bis zum Auftreten des Randknopfs, dauerte im Durchschnitt 3 Tage. Am 5.—6. Tage begann die Ausbildung des Vorderendes des Embryonen und zeigte sich die Medullarfurche, auf welcher in

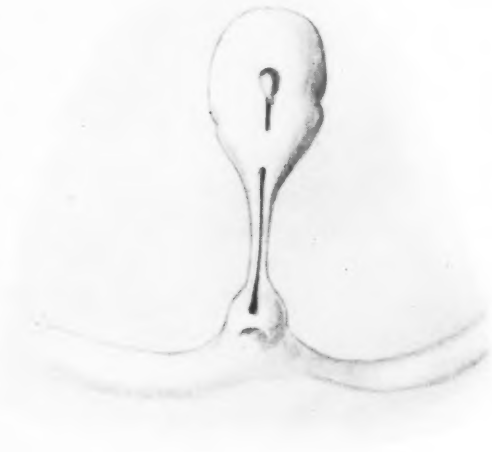

Abb. 2. Bastardembryo (27 Tage alt).

mehreren Fällen deutliche Wucherungen von pathologischen Charakter schon in toto bemerkt werden konnten. Die Weiterentwicklung ging ungleichmässig vor sich. Während bei vielen Exemplaren die äussere Form sich wenig veränderte und dieselben klein blieben, fuhren andere fort zu wachsen und es bildete sich bei ihnen Anzeichen einer Differenzierung des Vorderendes (Abb. 2). Bei vielen Embryonen konnte jedoch das Fehlen des Randknopfs wahrgenommen werden, und gleichzeitig gingen die Verdickungen des Embryonalschildrandes unmittelbar in die Medullarwülste des Embryos über (Abb. 3, 4 und 7). Bei einigen Exemplaren befand sich der Randknopf ausserhalb des verdichten Embryonalschildrandes, hinter dem Hinterende des Embryos, und von demselben zog sich über der Mediallinie des Embryos ein dunkler Streif nach vorne (Abb. 10, 11). Zu beachten ist ferner, dass Embryonen von verschiedenem Aussehen (Abb. 4 und 7), wie es sich an den Schnitten erwies, einen gleichen inneren Bau besassen und dass in einigen Fällen äusserlich weniger entwickelte Embryonen eine grössere Differenzierung aufwiesen, als andere, von denen sie ihrem Aussehen nach überflügelt worden waren. Deshalb wird es im weiteren Verlauf der Beschreibung praktischer sein, die Embryonen unabhängig von ihrem Alter zu betrachten, und dazu die in ihrer Entwicklung am weitesten vorgeschrittenen Exemplare auszuwählen.

Abb. 3. Bastardembryo (29 Tage alt).

Bei den am stärksten differenzierten Exemplaren finden wir folgende Embryonalanlagen: von denjenigen ektodermalen Ursprungs: den Nervenstrang mit den Vorder- und Hinterhirnanlagen, kompakte Augenanlagen, Anlagen der Ohrblasen und der Kopfnerven. Die Chorda ist bei allen Exemplaren ausgebildet. Das Entoderm in Gestalt einzelliger, selten zweizelliger Schicht, liegt dem zahlreiche normale Kerne enthaltendem Parablasten an. Im Mesoderm sind nur bei einigen Exemplaren auf den Querschnitten die Somiten von den Seitenplatten gesondert. Von der Bildung der Somiten kann aber noch nicht gesprochen werden, denn eine Segmentation des Mesoderms lässt sich weder in toto noch an den Längsschnitten wahrnehmen. Bei einem

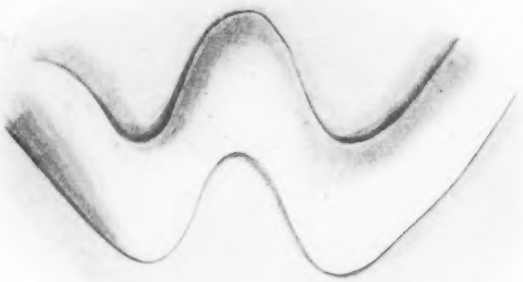

Abb. 4. Bastardembryo (32 Tage alt).

Exemplar ist auf Querschnitten die offenbar dem Zwischenmesodern entsprechende mesodermale Masse (masse intermédiaire, BRACHET, 1900) zu sehen (Abb. 5).

Im Vergleich mit den Coregonus- und Forelle-Embryonen der Kontrolle lassen sich bei den von uns untersuchten Exemplaren der Bastardembryonen eine Reihe von Abweichungen in der Ausbildung ausführen, die sich in folgendem äussern: 1. allgemeiner stark verlangsamter Entwicklungstempo;

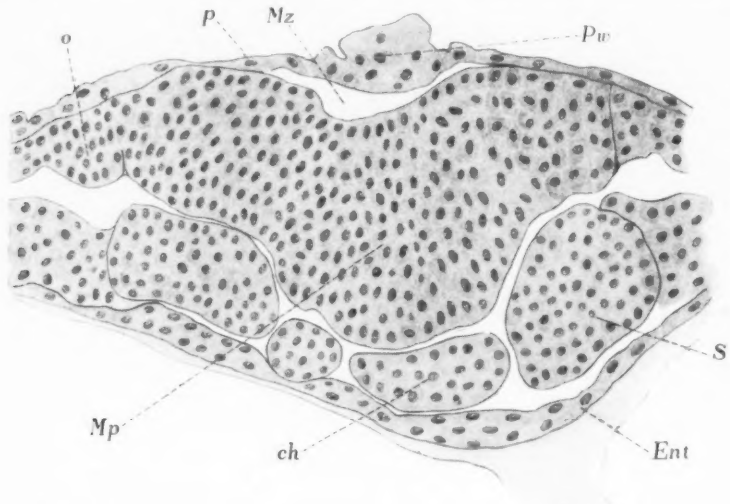

Abb. 5. Querschnitt durch den Embryo (Abb. 3) in der Gegend der Hinterhirnanlage. *Mz* — Medullarrinne; *p* — Periderm; *Pw* — Peridermwulst; *o* — Ohranlage; *Mp* — Medullarplatte; *S* — Somit; *ch* — Chorda; *Ent* — Entoderm.

2. Zurückbleiben in der Ausbildung der hinter der Erweiterung des Vorderhirns gelegenen Anlagen in Vergleich zum vorderen Teil des Embryos; 3. der Anordnung der Zellen im Gebiet des Randknopfs; 4. der Entwicklung der Nervenanlage; 5. der Entwicklung des Periderms.

1. Besonders auffällig ist die Verlangsamung im Entwicklungstempo während der Furchungsperiode, welche ungefähr 3—4mal mehr Zeit braucht als bei den Embryonen der Kontrolle. Die Gastrulationsperiode verläuft ebenfalls 3—4mal langsamer. Das weitere Entwicklungstempo hängt mit dem Auftreten von Abweichungen von der Norm zusammen.

2. Das Zurückbleiben in ihrer Entwicklung der verschiedenen Anlagen bei den Bastardembryonen äussert sich darin, dass das Mesoderm bei ausgebildetem vorderen Teil des Gehirns mit Augen und Nervenanlage keine Somiten bildet, die Chorda das Gehirn bei weitem nicht erreicht, die hinteren Gehirnteile nicht zu sehen sind und die Ohranlagen sehr schwach ausgebildet sind. Dagegen sind bei den Embryonen der Kontrolle in den entsprechenden Sta-

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dien die hinteren Gehirnpartien und Ohranlagen in toto erkennbar und an Schnitten auch einige der ersten Somiten (OELLACHER, Abb. 10, 6, HENNEGUY, Stad. D. u. F.) zu sehen.

3. Im hinteren Abschnitt des Embryos, im Gebiet des Randknopfes, entstehen bei der Forelle (OELLACHER, HENNEGUY, ZIEGLER) und Coregonus die Anlagen des primären Entoderms und des Nervensystems aus der Gesamtmasse der Zellen, welche in den Querschnitten eine konzentrische Anordnung besitzen. Mehr nach vorne tritt in diesem Zellenstrang (im Querschnitt) die den unteren Teil desselben, das Entomesoderm, von der höher gelegenen Nervenanlage trennende Querspalte auf. HENNEGUY erklärt diese Querschnittbilde dadurch, dass das primäre Ektoderm, indem es sich nach innen einbiegt, unmittelbar unter der Aussenschicht wächst, wodurch an der Stelle der Umbiegungen, die Zellen eine konzentrische Anordnung erhalten. Bei den Coregonus- und Forelle-Embryonen der Kontrolle lassen sich dieser Achsenstrang und seine nachfolgende „Segregation" in der Tat gut wahrnehmen. Bei den Bastarden war eine solche Anordnung der Zellen nicht zu bemerken. Offenbar findet hier ein Aufenthalt in der Entwicklung statt, was das erwähnte fehlende Hervortreten des Randknopfs zur Folge hat. Anstatt einer Erhebung dieses Gebietes über die Oberfläche des Dotters (Blastoderms) sieht man hier auf dem Längsschnitt (Abb. 8) gleichsam eine Einsenkung und eine entsprechende Loslösung von dem den Embryo bedeckendem Periderm.

4. Von grösserem Interesse ist für uns der Unterschied in der Entwicklung des Nervenstranges selbst. Das Nervensystem entsteht bei der Forelle in Form einer festen Anlage, deren Ränder zu Wülsten auswachsen. Diese Verdickungen erheben sich über den zentralen Teil und erwecken den Eindruck einer Vertiefung längs der Mittellinie des Nervenstranges. Äusserlich tritt diese als Medullarfurche in Erscheinung. Doch lässt sich an den

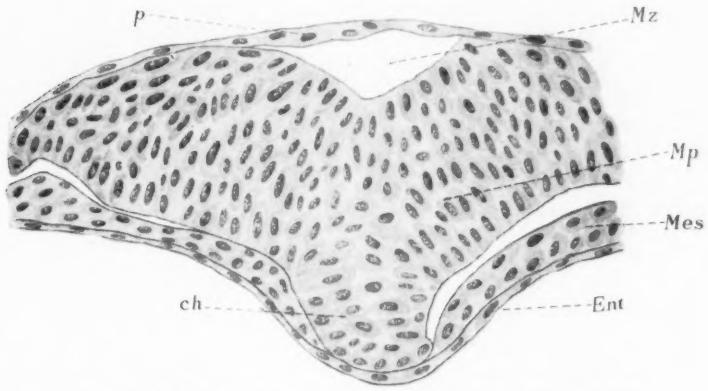

Abb. 6. Querschnitt durch den hinteren Teil des Embryos.

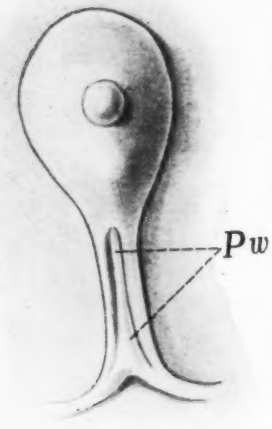

Abb. 7. Bastardembryo.

Schnitten deutlich erkennen, dass die Nervenanlage keineswegs eine Vertiefung besitzt (OELLACHER, ZIEGLER, HENNEGUY). HENNEGUY (1888, S. 535) betont, dass das Periderm an den Zellen der Nervenanlage fest anliegt und sich niemals von demselben loslöst. Dasselbe ist bei Coregonus der Fall. An den Schnitten durch den Embryo von Coregonus und der Forelle kann man in der Tat sehen, dass der Nervenstrang keine Furche besitzt. Dagegen lässt sich bei allen Bastarden auf der ganzen Strecke vom Beginn des Gehirns an bis zum hinteren Ende, oder in einzelnen Bezirken, eine gut ausgeprägte Vertiefung in der Nervenanlage deutlich wahrnehmen. Zugleich liegt das Periderm stets über der Vertiefung, indem es zwischen den erhöhten Rändern des Nervenstranges gleichsam eine Brücke bildet (Abb. 6). An dem Längsschnitt (Abb. 7) ist zu sehen, dass das Periderm am hinteren Ende hoch über dem Nervenstrang gelagert ist und nur unweit vom Vorderende über der Erweiterung des Gehirns mit ihm zusammentrifft.

5. Ausser dieser Abweichung von der für Coregonus und der Forelle typischen Lage des Periderms und der Nervenanlage verdient der ganz verschiedene Verlauf der Entwicklung des Periderms der Beachtung. Über der Vertiefung im Nervenstrang waren, wie schon erwähnt, bei der Be-

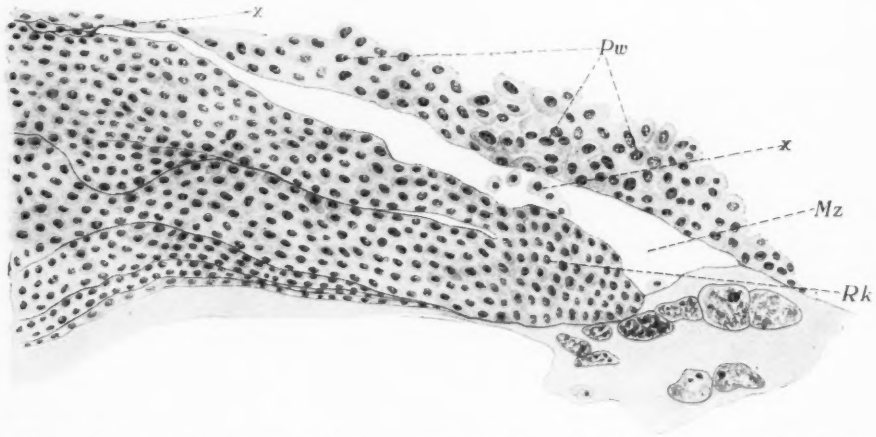

Abb. 8. Medianschnitt durch den Embryo (Abb. 7). *Rk* — Randknopf; *x* — eindringende Peridermzellen.

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trachtung der Bastarde in toto an Stelle der Medullarfurche Zellenwucherungen (Abb. 10 u. 11) bemerkt worden. Bei einigen Exemplaren bedeckten dieselben die ganze Medullarfurche, welche infolgedessen den Eindruck eines hervortretenden Stranges machte. Bei anderen Exemplaren kamen diese Wucherungen nur auf einigen Teilen des Medullarstreifens vor, indem sie gleichsam mit flachen oder vertieften Partien abwechselten. An den auf Abb. 7, 10 u. 11 wiedergegebenen Exemplaren ist deutlich zu sehen,

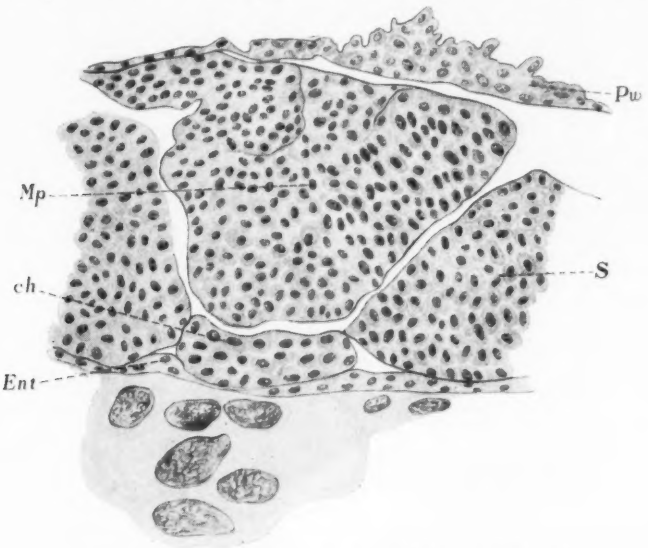

Abb. 9. Querschnitt durch den Embryo (Abb. 2).

dass dieser äussere Zellenstrang im Gebiet des Randknopfes an der Grenze der verdickten Rändern des Embryonalschilds beginnt, sich über der Medullarfurche ausbreitet und bis zur Gehirnweiterung reicht. Der Randknopf fehlt bei diesen Embryonen und wird bei einem derselben (Abb. 10) durch die Zellenwucherung nachgeamt. Diese Wucherungen sind hinter der Gehirnblase zu sehen und liegen, mit Ausnahme eines Falls, längs der Mittellinie, und bei einem Exemplar (Abb. 2) auch auf dem Gehirn. An Querschnitten im entsprechenden Gebiet lässt sich deutlich sehen (Abb. 9 u. 13), dass die erwähnten Auswüchse tatsächlich Wucherungen des Periderms bilden, dessen Zellen längs der Mittellinie ihre epithelartige Anordnung verlieren, von rundlicher Form sind und im mehreren Reihen lagern. Die Grösse dieser Zellenhäufungen variiert, doch nimmt dieselbe in der Richtung zum vorderen Ende stets ab. An der Stelle, wo das Periderm an das Nervensystem herantritt, haben seine Zellen gleichfalls eine unregelmässige rundliche Form und sind in 1—2 Reihen gelagert. Nur im Gebiet des Gehirns fehlen diese Ansammlungen und das ganze Periderm erscheint als typische flache einzellige Schicht.

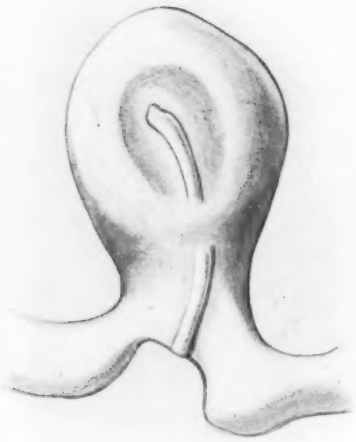

Abb. 10. Bastardembryo.

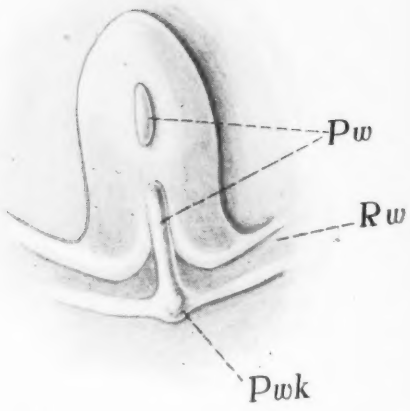

Abb. 11. Bastardembryo (35 Tage alt). *Pwk* — der von Peridermzellen imitierte „Randknopf"; *Rw* — Randwulst.

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An dem Längsschnitt (Abb. 8) ist diese Verteilung der über dem Embryo liegenden Zellenmasse sehr deutlich zu sehen. Offenbar beginnt ihr Wachstum am hinteren Ende und setzt sich in der Richtung nach dem Kopf fort. Wie auf derselben Abbildung zu sehen, bildet die Quelle der beschriebenen Zellenmassen das Periderm selbst, indem es stark anwächst. Die Zellen der peridermalen Wucherung sind äussert charakteristisch. Dieselben zeichnen sich durch ungleiche Grösse, unregelmässige rundliche Form und regellose An-

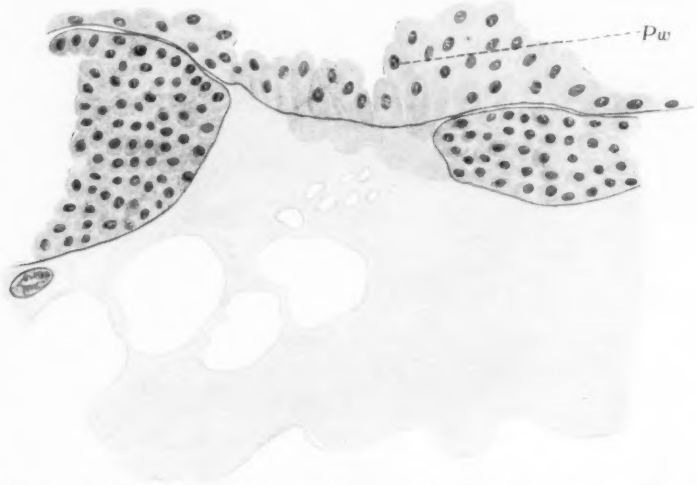

Abb. 12. Querschnitt durch den Embryo (Abb. 3) hinter dem Randknopf.

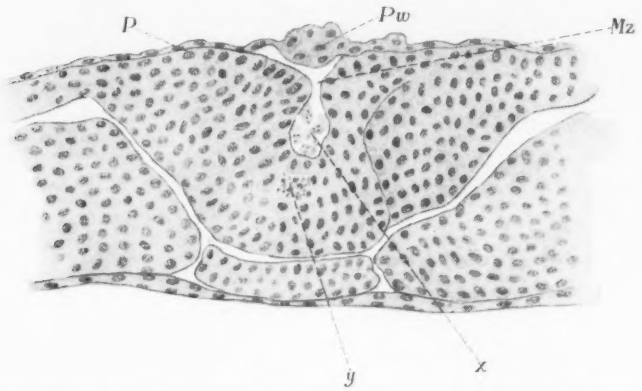

Abb. 13. Querschnitt durch den Embryo (Abb. 4); *x* — eindringende Peridermzellen; *y* — abgestorbene Zellen der Medullarplatte.

ordnung aus. Ihre Kerne sind bedeutend heller, als diejenigen der übrigen Zellen des Embryos und ebenso von ungleicher Grösse (Abb. 20).

Erinnern wir uns daran, dass bei der Mehrzahl der Bastarde am Hinterende des Embryos kein Randknopf zu sehen ist und dass die Verdickungen des Randes des Embryonalschilds unmittelbar in die Medullarwülste übergehen (Abb. 3, 4). Topografisch wird das dem Randknopf entsprechende und denselben, zuweilen seinem Aussehen nach, imitierende Gebiet von der Hauptzellenmasse der Wucherung, welche rückwärts über den Schildrand reicht, eingenommen. Auf Abb. 12, wo der Schnitt durch den hinteren Teil des Embryos dargestellt ist, erkennt man, dass in der Mittellinie ausschliesslich

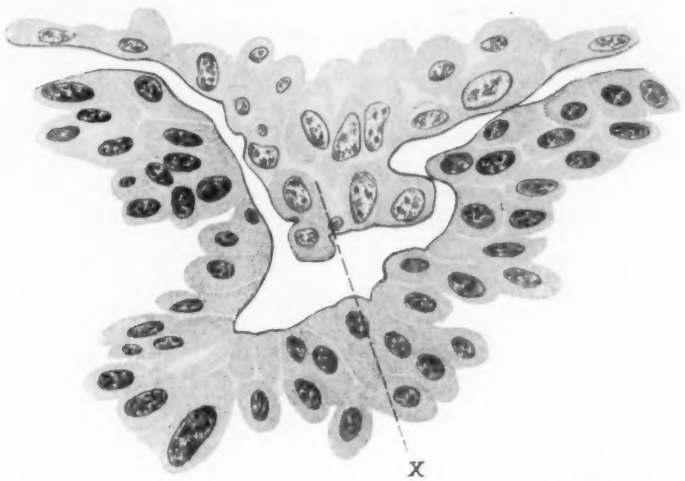

Abb. 14. Querschnitt durch den Embryo (Abb. 10) im Gebiet des Hinterhirns; *x* — eindringende Peridermzellen. ($^1/_{12}$ Imm.)

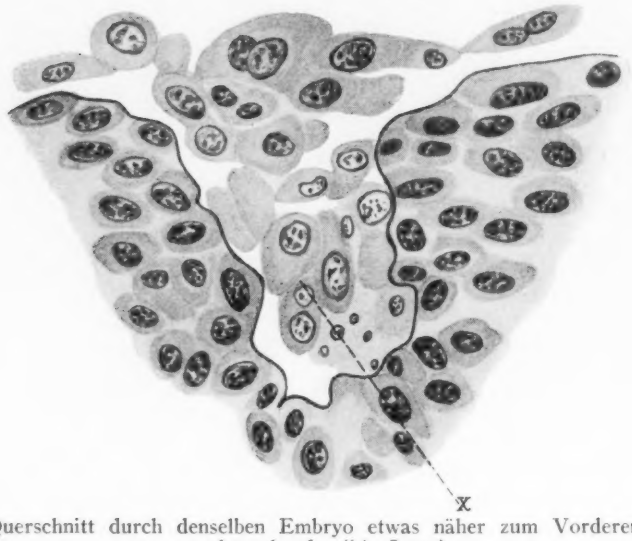

Abb. 15. Querschnitt durch denselben Embryo etwas näher zum Vorderende als der vorhergehende. ($^1/_{12}$ Imm.)

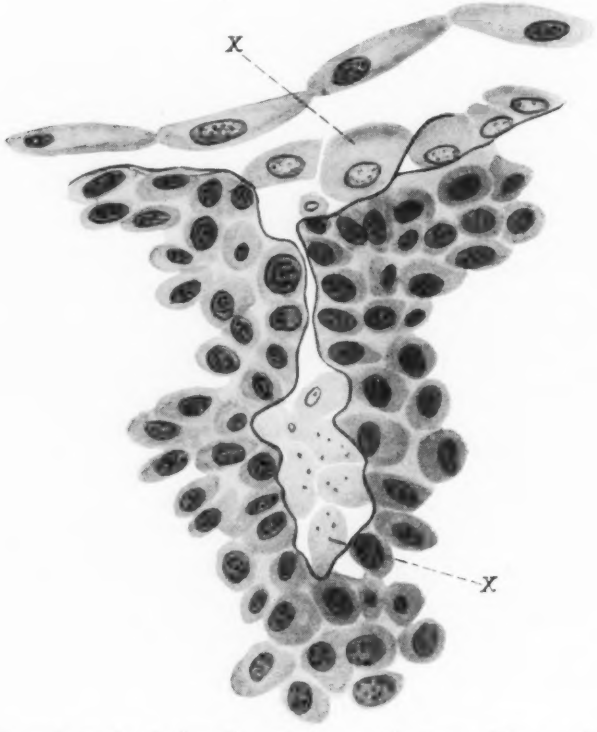

Abb. 16. Querschnitt durch denselben Embryo noch etwas näher zur Vorderende. ($^1/_{12}$ Imm.)

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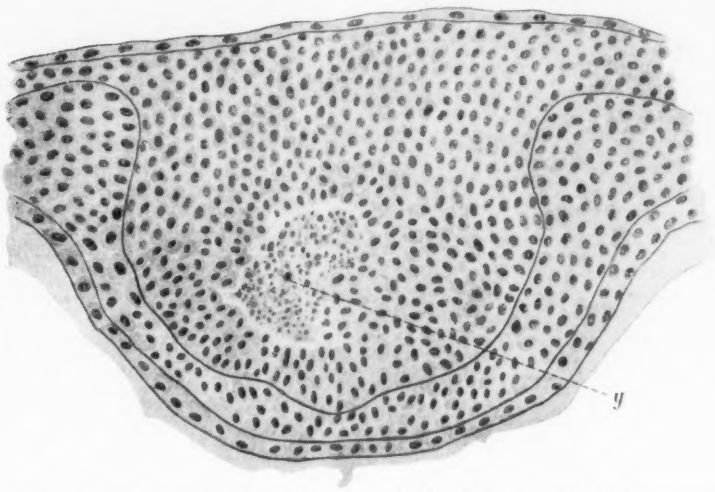

Abb. 17. Querschnitt durch den Embryo (Abb. 4) in der Vorderhirngegend.

Zellen der Wucherung liegen, während zu beiden Seiten sich die mesodermalen Zellmassen befinden.

Somit wachsen die Peridermzellen auf der Oberfläche der Keimscheibe und ist dieses Wachstum, da dieselben durch die übrigen Gruppen der Keimzellen nicht beeinflusst werden, regellos. Am Vorderende, wo der Medullarstrang an Grösse zunimmt und die Vorderhirnanlage bildet, steht das Periderm mit derselben in Verbindung und nimmt die gewöhnliche Lage ein. Die Zellen der Wucherung berühren sich hier also unmittelbar mit dem Nervenstrang. Indem dieselben sich ausbreiten, beginnen sie in den Strang selbst, oder, genauer gesagt, in die Gehirnanlage hineinzuwachsen. Auf Abb. 13, 14, 15 u. 16 kann man das Eindringen der Wucherungszellen in das Innere des Gehirns sehen. Abb. 15 u. 16 lassen erkennen, dass die eingewachsenen Zellen ihre Umgrenzung einbüssen und degenerieren, wobei gleichzeitig in diesem Abschnitt die

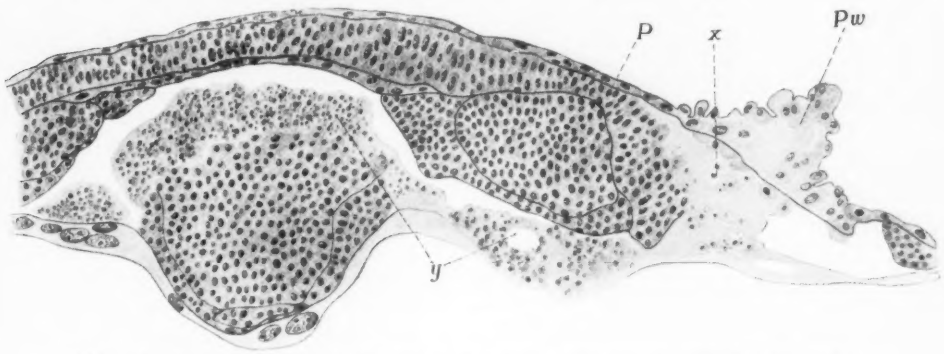

Abb. 18. Querschnitt durch denselben Embryo etwas weiter vom Vorderende.

Peridermzellen zu Grunde gehen. Hier sitzt unzweifelhaft eine Stöhrung der Lebensprozesse in der Nervenanlage ein. In Verbindung mit der Einwirkung der hineinwachsenden Zellen steht offenbar die hinten und oben beginnende und sich nach vorne und in die Tiefe der Gehirnanlage ausbreitende Degeneration und das Absterben der Gehirnzellen, wie dieses Abb. 17 u. 18 veranschaulichen. Auf einer dieser Abbildungen (Abb. 18) sind in der Gegend der Ohrblasen noch zwei symmetrisch liegende Herde der Wucherungszellen zu sehen und in derselben Gegend bemerkt man auch das Absterben der tiefer gelegenen Zellen des Embryos.

5. BESPRECHUNG DER BEFUNDE.

Das angeführte Untersuchungsmaterial gestattet uns an die Analyse der den Bau der Bastardembryonen charakterisierenden Deformationen heranzutreten und ihre Lebensunfähigkeit zu erklären. Obgleich wir gesehen haben, dass der Gastrulationsprozess bei den Bastarden scheinbar normal verlief und sich von der Kontrolle nur durch sein verlangsamtes Tempo unterschied, sind wir dennoch der Ansicht, dass es gerade diese Periode ist, in welcher die Ursache der anormalen Organogenese ihren Anfang nimmt. Die Verzögerung in der Entwicklung des Randknopfgebiets des Embryonalschildes wird durch die der Differenzierung der Zellen in die Keimblätter vorhergehenden vorbereitenden Prozesse bedingt. Indessen führt der Schild fort zu wachsen und seine Ränder überwachsen immer mehr den Dotter. Der Randknopfengebiet des Embryonalschildes bleibt infolge der beginnenden Organanlagendifferenzierung in diesem Prozesse und liegt nun vor der allgemeinen Grenze des Schildes. Je kleiner nun die Oberfläche des Dotters und je mehr die Randknopfformation verlangsamt ist, desto kürzer ist der Embryo zu dem Zeitpunkt, wenn sich der Blastopor schliesst. Hierin liegt, nach unserer Ansicht, die Erklärung der Mehrzahl der von allen Autoren beim Bastardembryo beschriebenen Verkürzungen des Körpers. Dieselbe Erklärung gilt für den von MOENKHAUS beschriebenen Fall bei den Bastarden Fundulus $\times$ Tautoga, wo es bis zum Abschluss des Blastoporus überhaupt zu keiner Bildung eines Embryokörpers kam. Ebenso erklären wir einige Fälle der Missbildung bei den Bastarden unserer Kreuzungen (Abb. 4).

Die Differenzierung des Embryokörpers beginnt mit dem Vorderende. Deshalb sieht man bei den entstehenden verkürzten Embryonen der Bastarde stattfindende Entwicklung des Vorderhirns und der mit demselben zusammenhängenden Gebilde (Augenblasen, Nervenanlagen usw.), während die hinteren Gehirnteile und Somiten noch unentwickelt bleiben. Aus diesem Grunde findet das von uns erwähnte Missverhältnis in der Ausbildung der einzelnen Teile des Embryos statt und entstehen Embryonen bei denen, in

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Anwesenheit eines ausgebildeten vorderen Teils, die äussere Gesamtform ganz undifferenziert ist. Da die Verzögerung in dem Gastrulationsprozess nicht bei allen Embryonen die gleiche ist, so sind der Grad der Differenzierung und der Charakter der Missbildungen bei gleichalterigen Embryonen verschieden. Die Verlangsamung in den vorbereitenden Zellprozessen während der, der Gastrulation unmittelbar vorhergehenden Periode hat eine weitgehende Veränderung der ganzen darauffolgenden Organogenese zur Folge, indem dieselbe nicht nur deren Verzögerung hervorruft, sondern mannigfaltige Missbildungen verursacht. Ganz zuerst wird sich dieselbe morphologisch in Defekten oder der Abwesenheit eines Randknopfs äussert.

Die Verlangsamung des Gastrulationsprozesses ist jedoch nicht die einzige Ursache der Abweichung der Embryonen von dem normalen Entwicklungsgang und erklärt in unserem Falle noch nicht das Absterben derselben während der beschriebenen Stadien. Eine zweite Quelle der Einwirkung auf die Entwicklung der Bastarde bildet die peridermale Zellschicht, in deren Ausbildung sehr grosse Abnormalitäten zu beobachten sind.

Das Periderm, als Embryonalorgan, entsteht während des Gastrulationsprozesses, indem es sich von den unter demselben liegenden Zellen des primären Ektoderms absondert. Das in einem so frühen Entwicklungsstadium entstehende Periderm nimmt im weiteren keinen unmittelbaren Anteil an den Umgestaltungen der Ektodermanlage und bleibt lange Zeit unverändert. Deshalb betrachten wir das Periderm als ein, während der Gastrulationsperiode völlig differenziertes, Organ.

Das normal wachsende Periderm folgt in seinem Wachstum den Rändern des Embryos. Infolge des Zurückbleibens des Randknopfs in einem Vorrücken bei den Bastarden wächst hier das Periderm rückwärts von der Embryonalkörperanlage und überzieht den Dotter im Zwischenraum zwischen den hervortretenden Rändern des Schilds. Da der Randknopf sich kaum über dem Niveau des Dotters erhebt und zuweilen in denselben eingesenkt ist, während das Periderm sich auf den Dotter stützt, so bleibt zwischen dem Periderm und dem Randknopf ein freier Raum. Bei fortschreitendem Wachstum des Embryos und dem Entstehen der Vertiefung der Medullarfurche in demselben, spannt sich das Periderm gleichsam über der Furche und berührt sich in der Mittellinie mit dem Embryo nur ins Gebiet des stark hervortretenden Vorderhirns. Somit entstehen, längs der ganzen Medullarfurche und rückwärts von derselben, für die Entwicklung des Periderms ungewöhnliche Verhältnisse, insofern dasselbe mit den darunterliegenden Zellen nicht in Berührung steht (Abb. 8).

Die Weiterentwicklung des Periderms im genannten Gebiet des Embryos hängt mit dem Charakter seiner Zellen beim Bastard in Verbindung. Durch den Vergleich des Periderms bei den Bastarden mit denjenigen bei der Kontrolle lässt sich feststellen, dass die Peridermzellen des Bastards von den-

jenigen des Coregonus verschieden sind und mehr an die Peridermalzellen der Forelle erinnern. Auf Abb. 19 sind die, bei gleicher Vergrösserung gezeichneten, gleich langen Stücke des Periderms bei Coregonus, Forelle und dem Bastarde Coregonus × Forelle wiedergegeben. Wie aus der Zeichnung zu sehen ist, sind die Zellen von Coregonus grösser und flacher als diejenigen der Forelle. Innerhalb des gleichen Abschnitts beträgt die Anzahl der Zellen bei Coregonus nur 7—8, wogegen sie bei der Forelle zwischen 12—15 schwankt. Wenn man berücksichtigt, dass die Eier von Coregonus denjenigen

Abb. 19. Die Peridermzellen. *A* — Coregonus lav.; *B* und *C* — Bastard; *D* — Salmo trutta.

der Forelle an Grösse nachstehen, so muss daraus gefolgert werden, dass die Peridermzellen bei Coregonus sich langsamer als bei der Forelle vermehren.

Bei den Bastarden tragen die Peridermalzellen denselben Charakter wie diejenigen der Forelle und offenbar ist auch das potentiale Tempo ihrer Teilung bei beiden das gleiche. Wir können sagen, dass der Bastard das *väterliche* Periderm geerbt hat. Dieses scheint uns möglich, da das Periderm, wie bereits bemerkt, ein *differenziertes* Organ ist, und deshalb stossen wir bei demselben zum ersten Mal auf das Faktum der Vererbung.

Erinnern wir uns daran, dass die früheren Autoren über die Vererbung der väterlichen Züge nach solchen Merkmalen wie das Pigment urteilten. Das bei Fundulus sehr früh auftretende Pigment diente für MOENKHAUS, NEWMAN, BANCROFT u. a. als Anzeichen der Vererbung. Die Pigmentzellen sind jedoch differenziert. Wenn diese Autoren unter den Organen des Embryos kein Objekt finden, an dem in den frühen Stadien die väterlichen Merkmale zum Ausdruck kommen konnten, so sehen wir in unserem Fall, dass das Periderm ein solches, der Zeit nach erstes, Organ ist, an dem sich diese Tatsache feststellen lässt.

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Der dem väterlichen Typus eigene Charakter des Periderms beim Bastard ruft ein Missverhältnis zwischen der Anzahl der entstehenden Peridermzellen und der Grösse des Coregonuseies hervor. Es besteht ein potentialer Überfluss von Peridermzellen und unter entsprechenden Verhältnisse wird diese Möglichkeit zur Tatsache.

An unseren Präparaten haben wir oberhalb des gastrulierenden Teils des Schildes und der Medullarfurche lokalisierte Anhäufungen von Peridermal-

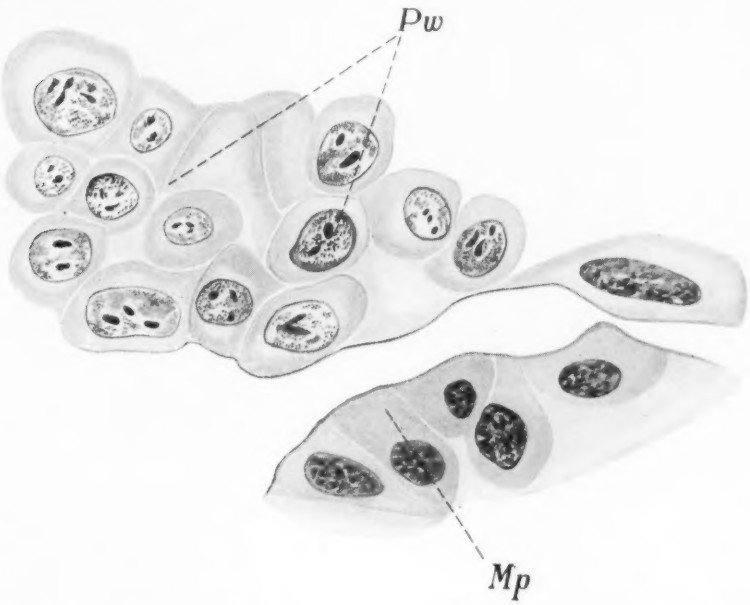

Abb. 20. Querschnitt durch die Peridermwulst (Obj. $^1/_{12}$), den Charakter der Zellanordnung zeigend. ($^1/_{12}$ Imm.)

zellen gesehen. Offenbar gibt es hier die entsprechende Anregung, welche, wie uns scheint, in dem Fehlen von unmittelbar dem Periderm anliegenden Zellen besteht.

Aus den Arbeiten HOLTFRETERS (1933) ist bekannt, dass die epitheliale Anordnung der Ektodermzellen bei dem Froschembryo das Resultat der Einwirkung der darunterliegenden Mesodermalzellen bildet. In Abwesenheit von darunterliegendem Zellen zeigte das Ektoderm bei den Versuchen HOLTFRETERS regelloses Wachstum, die Zellen desselben waren von unregelmässiger rundlicher Form und ungleicher Grösse. Offenbar bedingte auch bei den Bastarden zwischen Coregonus und Forelle das Fehlen des Kontaktes zwischen Randknopf und Periderm das pathologische Wachstum des letzteren, indem dasselbe sich natürlicherweise über der Medullarfurche ausbreitete, da hier, auf den ganzen Strecke, das Periderm mit den darunterliegenden

Zellen nicht in Berührung kommt. Über den Medullarwüsten und im Gebiet des Vorderhirns, wo das Periderm die Ektodermzellen unmittelbar bedeckt, nimmt dasselbe die gewöhnliche epitheliale Lage ein. Somit hatten die Mangel in der Ausbildung des Randknopfs vor allem ein regelloses Wachstum des Periderms über demselben hervorgerufen. Infolgedessen finden wir bei der Mehrzahl unserer Bastarde auf dem Epiderm eine grosse dem Randknopf nachgebildete Wucherung. Bei fortgesetzter Entwicklung des Embryos diente diese anfängliche Wucherung als Herd regellosen Wachstums längs der ganzen Medullarfurche. Hierbei wachsen die Zellen zum Teil in den Raum unter derselben hinein (Abb. 8 u. 13) und im Gebiet des Gehirns in dasselbe hinein. Das Hineinwachsen der Peridermalzellen in die Nervenanlage fängt, wie dieses die Schnitte (Abb. 17 u. 18) bestätigen, von hinten und von oben an und setzt sich in der Richtung nach vorne und ventral fort. Dadurch wird vor allen Dingen das Absterben der Zellen der Nervenanlage im Gebiet des künftigen Hinterhirns hervorgerufen. Die Verletzung der Integrität dieses Gebiets muss, gemäss den Angaben SUMNERS (1903), die Differenzierung der hinteren Gebiete zum Stillstand bringen und ein Missverhältnis zwischen denselben und dem Vorderende hervorrufen.

Somit besitzen wir in diesem Prozess des Hineinwachsens der Peridermzellen in die Nervenanlage noch eine mögliche Ursache von Missbildungen bei den Bastarden.

Doch hat die Einbürgerung der Peridermzellen mit der Zeit noch grössere nekrotische Veränderungen sowohl in dem hineinwachsenden Periderm selbst als auch in den übrigen Zellen des Gebietes, wo das Hineinwachsen stattfindet, zur Folge, indem es den Untergang und Tod des Embryos hervorruft.

Interessant ist es, dass bei reziproken Embryonen gleichfalls eine anormale Entwicklung des Periderms beobachtet wird, indem dasselbe an der Oberfläche des Embryos faltet und Stränge bildet. Doch tragen die peridermalen Auswüchse bei den Bastarden von Forelle × Coregonus einen ganz anderen Charakter und haben eine andere Lage. In diesem Falle fehlen die von uns für die Bastarde von Coregonus × Forelle beschriebenen Verhältnisse und deshalb sind die Peridermalbildungen von anderer Art.

6. ZUSAMMENFASSUNG.

Die angeführten Tatsachen gestatten, aus den gemachten Beobachtungen folgende Schlussfolgerungen zu ziehen.

1. Eine Befruchtung von Coregonus-lav.-Baeri-Eiern mit dem Sperma der Forelle (Salmo fario), des Lachs (Salmo salar) und Salvelinus fontinalis findet unzweifelhaft statt und ist von einem wirklichen Vereinigung der Chromosomen begleitet.

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2. Das Entwicklungstempo der Bastarde ist sowohl während der Furchung, als auch der Ausbildung des Embryos stark verlangsamt.

3. Infolgedessen, dass die erste Entwicklungsperiode vor der Gastrulation und dergleichen der Anfang des Gastrulationsprozesses bei den Bastarden Coregonus × Salmo fario hinsichtlich der Zellprozesse äusserlich normal verläuft und keine sichtbaren Abweichungen von der elterlichen Formen aufweist, lässt sich die unvollständige Ausbildung der Bastarde durch Störungen während der Organogenese erklären.

4. Die Missbildungen entstehen infolge einer ungleichmässigen Entwicklung der Embryonalanlagen.

5. Die Hauptursache von Missbildungen bei den Embryonen besteht in der Verlangsamung des Gastrulationsprozesses, welche das Fehlen des Randknopfs oder seine verminderte Grösse und Lage vor dem Schildrand herbeiführt.

6. Gewöhnlich ist der Randknopf in seiner Entwicklung rückständig und im Zusammenhang damit äusserlich nicht wahrnehmbar, indem seine Zellen in einem gewissen Abstand vom Periderm liegen.

7. Eine der Ursachen der Missbildungen bei den Bastarden und ihres Zugrundegehens bildet offenbar der von den Bastarden ererbte Charakter und Teilungstypus des väterlichen Periderms, was zu dessen anormalen regellosen Wachstum führt.

8. Das anormale Wachstum des Periderms äussert sich in der Bildung von Auswüchsen längs der Medullarfurche und dem Eindringen ihrer Zellen in der Nerven-, speziell die Gehirnanlage.

9. Die Bastardnatur des Periderms äussert sich offenbar in den frühen Entwicklungsstadien in Zusammenhang damit, dass dasselbe zu dieser Zeit das einzige endgültig differenzierte Gewebe des Embryos ist.

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ZUM BAU DES PRIMORDIALCRANIUMS UND DES KOPFSKELETTES VON ABLEPHARUS PANNONICUS

VON

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(Aus dem Zoologischen Institut der Universität Jerusalem)

MIT 24 TEXTFIGUREN

Bei der Durchsicht einer Schnittserie von Ablepharus pannonicus fiel mir auf, dass viel mehr Teile des Primordialkraniums erhalten bleiben als bei anderen Reptilienschädeln. Zunächst schrieb ich dies dem Umstande zu, dass der Untersuchung ein zwar erwachsenes, aber nicht bemerkenswert grosses Tier zugrunde lag. Die Befunde wurden sodann an einem zweiten, verhältnismässig sehr grossen Exemplar ergänzt und die Ergebnisse der beiden Serien verglichen und weitgehendst übereinstimmend gefunden. Da meines Wissens sonst keine detailliertere Untersuchung über diesen Schädel vorliegt (LAKJER erwähnt nur flüchtig wenige Einzelheiten), übergebe ich die Ergebnisse dieser Untersuchung zur Publikation. Sie geben einige Hinweise auf das Entwicklungstempo des Schädels in den letzten Wachstumsstadien.

Das bezahnte, paarige Prämaxillare bildet den Vorderrand des Oberkiefers; dann sondert sich der Knochen in einen der Mittellinie genäherten septalen Teil und in die zahntragende Platte. Das ganz kurze Septum bildet

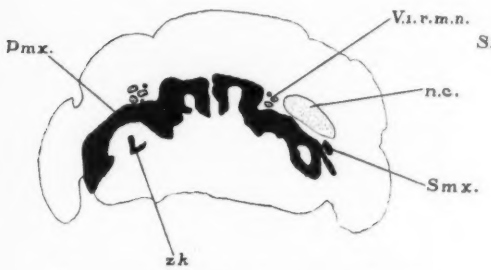

Fig. 1. Schnitt durch den vordersten Teil des Prämaxillare, Beginn der Nasenkapsel vor und über dem Nasenloch.

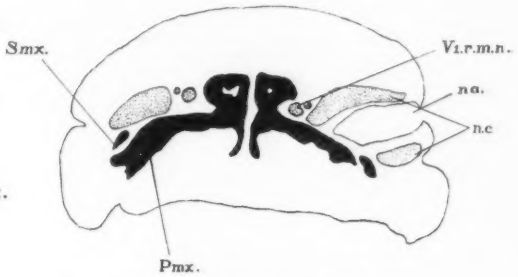

Fig. 2. Rechts: Bereich der äusseren Nasenöffnung; Beginn des Prämaxillarseptums.

den Übergang zu zwei dorsalen Platten, die durch das dazwischentretende Nasenseptum vom Alveolarteil getrennt bleiben. Die zunächst nur am Dach der äusseren Nasenöffnungen entwickelten Knorpelflügel der Nasenkapsel schliessen sich unmittelbar hinter der knöchernen Septalregion der Prämaxillaria (Fig. 1—4) zum Septum nasi, dem sich von ventral her das unpaare Prävomer anlagert. Knapp neben dem Beginn des Knorpelseptums liegt das Foramen apicale. Während sich unter die dorsalen Prämaxillarteile paarige Nasalplatten schieben, die zuerst lateral hervortreten (Fig. 5), erhöht und verschmälert sich das Septum nasi. An die Alveolarteile des Prämaxillare schliesst sich ventral vom Nasenloch von aussen her der Zahnteil des Supramaxillare an, während seitlich von dem Septum die Knochenblasen für das JACOBSOHNsche Organ, die Septomaxillaria beginnen, deren Oberrand den N. medialis nasi aufnimmt. Der Hinterrand der Nasenlöcher wird von einer kurzen Knorpelbrücke umspannt, der seitlich der Anfang der Nasendrüse anliegt (Fig. 5). Mit der Ausbreitung der Nasalia nach den Seiten geht ein dorsaler Durchbruch der Knorpelkapsel Hand in Hand (Fenestra dorsalis nasi, Fig. 6). Die ventrale Plattform des Septums (Fig. 4) ist im Bereich des Septomaxillare zu Ende, indem sich vom vertikalen Septum Seitenteile ablösen, die nunmehr den Boden der nur ganz rostral ringsum vom Septomaxillare umgebenen Nebennase bilden. Von diesem bleibt also im weiteren Verlauf ein kleiner septaler Anteil für die Passage des N. medianus nasi und eine Zwischenwand erhalten, die die Nasenhöhle von der Nebennase trennt (Fig. 6). Der ventral abgegliederte Knorpelteil entwickelt eine Muschel zur Stütze der pilzförmigen Erhebung vom Boden der Nebennase. Hinter diesem Wulst zieht sich der ventrale Knorpelstreif aus dem Organon vomeronasale nach lateral zurück und keilt sich zwischen diesem und der Nasendrüse ein (Fig. 7). An Stelle der ventralen Knorpelplatte tritt die

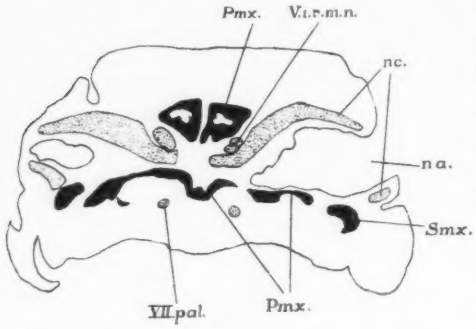

Fig. 3. Vereinigung der Flügelknorpel zum Septum nasi.

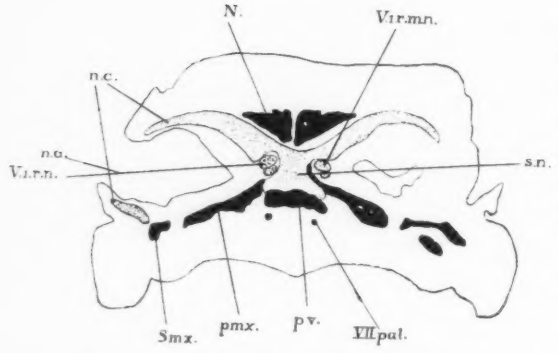

Fig. 4. Durchbruch des Nervus medialis nasi durch das Foramen apicale, Septum cartilagineum vollständig.

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verbreiterte Knochenwand des Prävomer, dessen aufsteigende Mittelleiste bis zum Unterrand des Nasenseptums reicht. Der Vergleich mit dem ZIEGLERschen Modell des Primordialkraniums eines Embryos von Lacerta agilis zeigt, dass durch Schwund der dorsolateralen Nasenkapselwand das obere und seitliche Nasenfenster verschmolzen sind (Fig. 6), und auch der N. lateralis nasi ohne Knorpelumrahmung lateral vom freien Rand des Nasale austritt. Der seitlich abgedrängte Bodenknorpel bildet hinter der Concha eine nach hinten offene Rinne, die den Vorderrand der STENSONschen Gänge umfasst und sich in gut ausgebildete Cartilagines ectochoanales fortsetzt; diese liegen in den Hautfalten, die medial von den Processus palatini des Maxillare vorspringen (Fig. 7). Wenn man von dem etwa I-förmigen Querschnitt des Nasenknorpels am Beginn der Kapsel ausgeht, zeigt sich, dass der dorsale Querbalken ohne besondere Differenzierungen bald aufhört und von den ventralen Differenzierungen durchwegs getrennt bleibt, wenn auch nur durch den schmalen Saum der Aussenkante des Septomaxillare (Fig. 6). Der ventrale Querbalken bildet jederseits den Boden der Nebennase bis zur Concha, die frei caudad vorspringt. Der Rest verlässt die Nebennase mit dem seitlichen Vorwachsen des Präwomer bis zum lateralen Rand des Septomaxillare, wobei die C. ectochoanalis als freier Fortsatz abgegliedert wird. Noch vorher beginnt der Processus frontalis des Supramaxillare (Fig. 7), der die Nasendrüse von aussen umwächst, wie der aufsteigende ventrale Knorpel von medial.

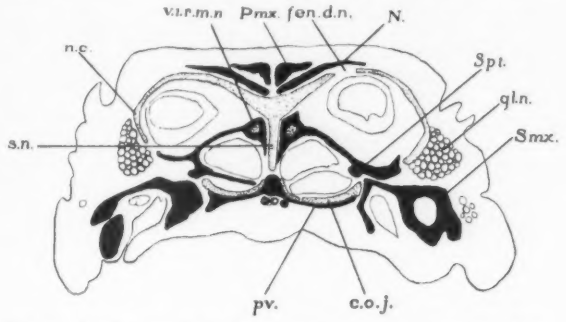

Fig. 5. Vorderer Teil des Organon vomero-nasale, das ventral von Knorpel umkleidet wird.

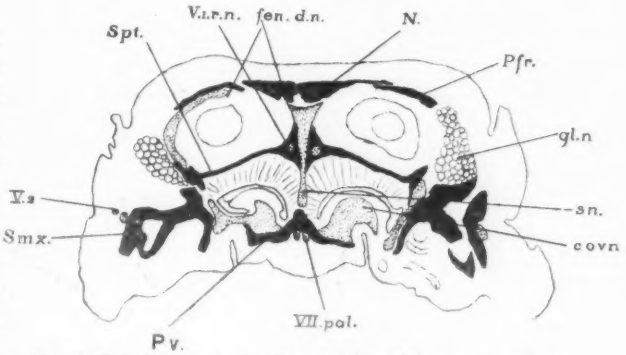

Fig. 6. Schnitt durch die Concha der Nebennase, grösste Ausdehnung des seitlichen Fensters der Nasenkapsel. Die Ventralwand des Septomaxillare ist zugunsten des Prävomer reduziert.

Erst an das Ende des Organon vomeronasale schliessen ohne Zusammenhang mit den Differenzierungen der Ventralplatte des vorderen Septal-

bereiches die stabförmigen Cart. paraseptales als freie Fortsätze an; sie liegen nahe am Ventralrand des Septum nasi (Fig. 9). In diesem Bereich ist die Nasendrüse nach aussen zu völlig durch das Nasale und Maxillare abgeschlossen, das Septomaxillare auf schmale septale Endplatten reduziert.

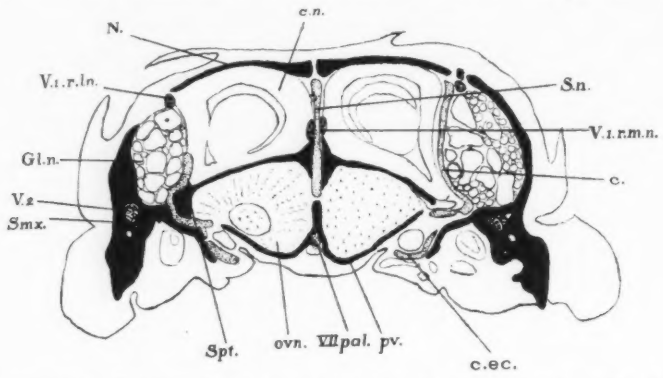

Fig. 7. Der ventrale Teil der Nasenkapsel gliedert die Cart. ectochoanalis ab. Austritt des Nervus lateralis nasi. Die Nasendrüse wird vom Processus ascendens maxillaris lateral umschlossen.

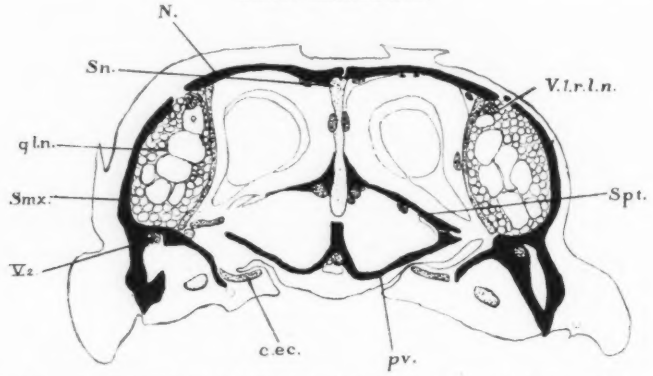

Fig. 8. Die frei vorspringenden Cartt. ectochoanales. Man sieht verschiedene Äste des Olfactorius im Bereich der Nasenschleimhaut und am Dach der Nebennase.

während aufsteigende Vomeräste den caudalen Teil des Organes unvollständig umgreifen und einen Raum für den dieses Organ versorgenden Nerven freilassen (Fig. 8, 9).

Zwischen Nasale und Maxillare beginnt in der Tiefe das plattenförmige Präfrontale, hinter den paarigen Nasalia das unpaare Frontale, das jene von medial her auseinanderdrängt. Während sich die knorpelige Seitenwand der Nasenkapsel vom Maxillare ventral etwas abhebt (Fig. 9), zweigt der Tränen-Nasengang vom ventralen Teil der Nasenhöhle (vordersten Teil des Choanenspaltes) ab, wobei er zunächst noch durch einen von dorsal vorspringenden Hautlappen vom eigentlichen Choanenspalt getrennt bleibt. Die

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anfangs leicht konkave seitliche Knorpelwand biegt nun scharf nach innen zur Bildung der Nasenmuschel, umgreift dabei sukzessive die Nasendrüse von innen her und gewinnt jetzt zum erstenmal dorsalen Anschluss an das Septum nasi (als Derivat des Knorpelbodens der Nasenkapsel). Mit dem Ende der Nasalia beginnt das Gebiet der Lobi olfactorii; damit löst sich die kurze dorsale Knorpelbrücke des Conchalabschnittes, wobei das Septum von oben her abgedrängt wird, sich also stark verschmälert (Fig. 10). Gleichzeitig steigert sich die conchale Einwölbung bis zum gänzlichen Umfassen des Caudalendes der Nasendrüse durch den Knorpel, wobei der Tränen-

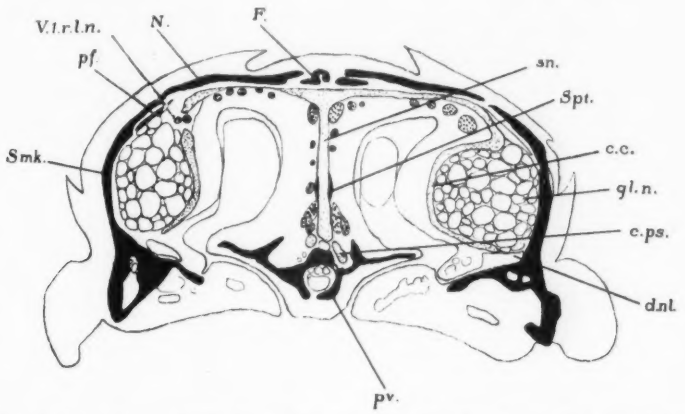

Fig. 9. Knapp hinter dem Organon Jacobsoni; Beginn der Cartt. paraseptales und des Frontale. Rechts Kommunikation des Ductus nasolacrymalis mit der Nasenhöhle und Choanenspalte. Vorwölbung der Concha in die Nasenhöhle, deren Knorpeldach wieder komplett ist.

Nasengang ventral zwischen Knorpel und Processus alveolaris maxillae zu liegen kommt und medial von einem Vorsprung der Knorpelkapsel begrenzt wird. Zwischen das sich verschmälernde Maxillare und das Frontale schiebt sich ein Keil des Präfrontale ein. Obzwar der Beschreibung dieser Region nur der jüngere Schädel zugrunde liegt, gilt sie bis in alle Einzelheiten auch für das grössere Tier. Wesentliche Unterschiede treten erst beim Übergang in die Orbitalregion auf.

Bei dem jungen und alten Exemplar treten hier oberhalb vom Vomer, das caudal einen dem ventralen Plattenteil parallelen Dorsalfortsatz abgibt, die vordersten Teile des Palatinum auf. In dieser Region tritt im Septum nasi ein Foramen auf. Die paarigen Endfortsätze des Prävomer spalten sich jederseits; aus einem dorsomedianen Kiel, dem ventral eine tiefe Furche entspricht, gehen also die oberen beiden der vier Endzipfel hervor, die den Endabschnitten der Cart. paraseptales angelagert sind. Beim Jungtier sind die Verhältnisse in dieser Region des Prävomer viel unklarer wegen Ausbildung unregelmässiger Kavernen in der zu zarten Bälkchen aufgelösten

Knochensubstanz; ein viel kleinerer Endabschnitt ist paarig und anstelle einer tief einschneidenden Ventralfurche ist ein stark vorspringender Kiel vorhanden (Fig. 10); die Dorsalfortsätze treten ebenfalls an die Enden der Paraseptalknorpel heran.

Im Gebiet der orbitalen Verschmälerung teilt sich der Ventralrand des Präfrontale in zwei Lamellen, die den Tränen-Nasengang zwischen sich fassen und ihn durch Schwund der äusseren in die Orbita eintreten lassen. Der Mittelteil des Präfrontale buchtet sich, die Hirnhöhle eng umgreifend,

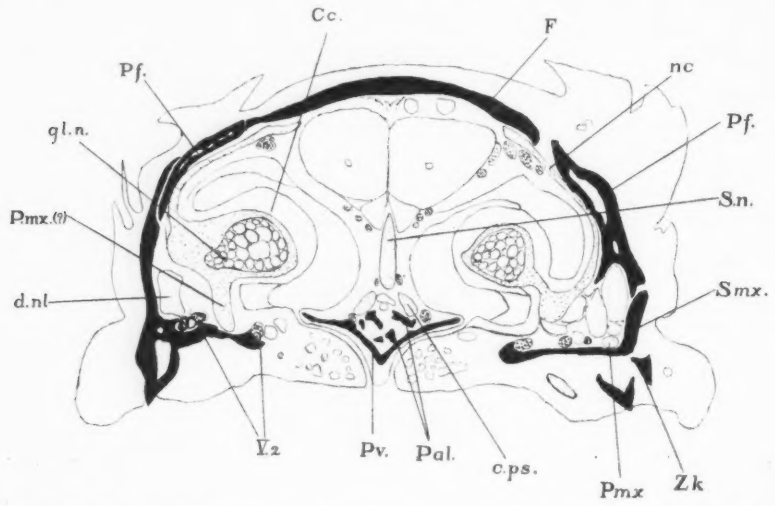

Fig. 10. Dorsaler Durchbruch der Nasenkapsel für den Bulbus olfactorius; die Nasendrüse ist allseits von Knorpel umschlossen. Oberhalb vom Prävomer Beginn rostraler Palatinabschnitte. Rechts: der isolierte Rest des primordialen Processus maxillaris in der Nische des Maxillare. Verkürzung des Nasenseptums.

stark ein. In den Winkel ist die Glandula Harderiana eingelassen (Fig. 12). Der frei vorspringende Orbitalwulst stützt eine Reihe verknöcherter Schuppen; darunter liegt beim Jungtier ein starker, dichter Bindegewebspolster mit kaum angedeuteten Spuren zentral beginnender Verknöcherung, beim erwachsenen Stück liegt hier ein voll ausgebildetes Supraorbitale, das somit erst spät verknöchert. Dem Knochenschuppenbelag eng angeschlossen endet es noch vor dem Augapfel. An das Maxillare lagert sich in der Verlängerung der äusseren ventralen Präfrontallamelle ein winziges Lacrymale an (Fig. 11, 12). Die Einengung des Präfrontale, die mit einem Vorwachsen der Gl. Harderiana in septaler Richtung Hand in Hand geht, zerlegt den Knochen in einen auf die Schädeldach-Aussenkante beschränkten dorsalen Sporn und einen kürzeren ventralen, der über dem lateralen Fortsatz des Palatinum an das Maxillare anschliesst. Das im Bogen die Choanenöffnung umspannende Palatinum reicht, durch V. 2 vom Maxillarrand getrennt, weit in die

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medialwärts gerichtete Gaumenfalte herein, die durch geringe Überlappung der freien Ränder einen fast geschlossenen Atemweg mit ihrem Partner bildet, der sich erst im caudalen Orbitalgebiet zu einem offenen Spalt erweitert (Fig. 12—15).

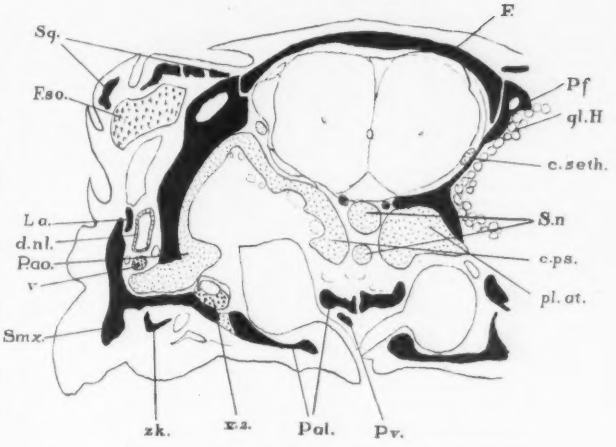

Fig. 11. Abzweigung der Commissura sphenethmoidalis vom Planum antorbitale (links), das (rechts) in der Cart. paraseptalis endet. Der Ductus nasolacrymalis verlässt die Orbita; lateral hievon das Lacrymale.

Hinter der Concha bleibt an der Medialfläche des Präfrontale (noch vor der eben genannten Einengung) ein Knorpelbelag erhalten, der nach Unterlagerung des Tränenganges den gesamten ventralen Hirnabschnitt umgreift und in der Cartilago paraseptalis endet (Planum antorbitale, Fig. 11). Deutliche Processus maxillares fehlen bis auf ein winziges, isoliertes Knorpelstück zwischen Palatinum und Maxillare (Fig. 10); doch könnte auch der ventrolaterale Teil des Planum antorbitale, der den Tränen-Nasengang knapp vor dem Übergang in die Orbita unterlagert, ein vorderer Rest des Maxillarfortsatzes sein. Vom Dache des Planum gehen Sphenethomoidkommissuren im vorderen Teil der Orbita in das mittlerweile wieder höhere und vollständige Interorbitalseptum über (Fig. 12). Beim Alttier ist der Maxillarfortsatz noch stärker reduziert und im Gebiet des Anschlusses des Planum an die Paraseptalknorpel ist jenes schon ganz vom Ventralrand des Präfrontale nach dorsal ausgebogen, so dass das dorsomediane Stück am weitesten caudad vorspringt.

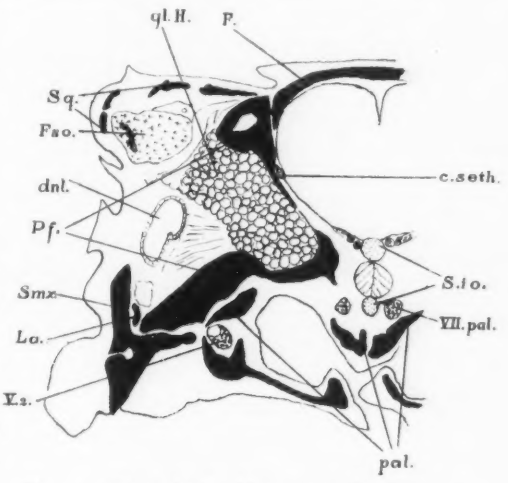

Fig. 12. Die orbitale Verengung des Präfrontale führt zur Zerlegung in zwei Fortsätze; nur Andeutung einer Verknöcherung im Gebiet des Supraorbitale.

Das Palatinum beginnt jederseits zwischen dem caudalen Fortsatzpaar des Prävomer mit zwei gesonderten Knochenbälkchen, die sich knapp hinter dem dorsalen Prävomerflügel über dem ventralen vereinigen. Diese medianen Fortsätze stellen wohl das

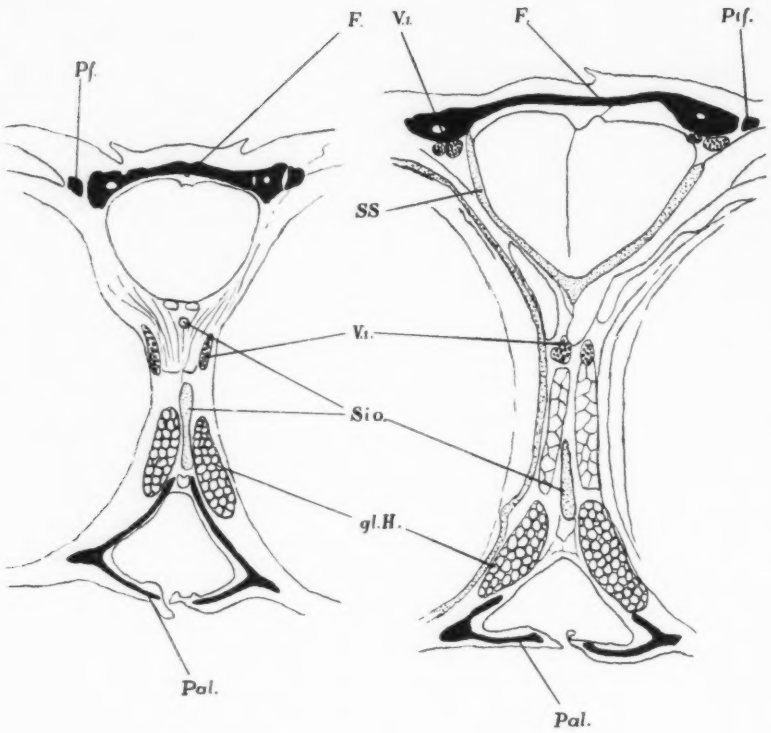

Fig. 13. Fig. 14.

Fig. 13. Schnitt durch das Gebiet der geringsten Interorbitalbreite; der obere Teil des Septums, der caudalwärts das Septum supraseptale liefert, ist nur ein runder Knorpelstab, der in der nächsten Fig. sich weiter ausdehnt.

Fig. 14. Das Septum supraseptale in seiner grössten Entfaltung, das Hirn bis zum Schädeldach umschliessend.

Hemipterygoid LAKJERS vor, doch ist die ganz eindeutige Zugehörigkeit zu dem übrigen Teil des Palatinum zu beachten, ein Befund, der für beide untersuchten Stücke zutrifft; auch weist im caudalen, einheitlichen Abschnitt nichts auf eine sekundäre Verschmelzung hin. Hinter dem Prävomer vereinigen sich der mediale und der dem Maxillare angeschlossene Abschnitt oberhalb von der Choane, nur der mediale Teil bleibt erhalten mit einer schräg zum Septum aufsteigenden Lamelle und einer annähernd horizontalen, die die Gaumenfalten stützt; die steile Lamelle klappt dann bis in eine zur unteren parallelen Richtung um und beide umgreifen von lateral das vorderste Pterygoidende. Das ganze Palatinum ist wie das Pterygoid überaus zart und unbezahnt. Im Gebiet der Bulbusmitte springt der Endteil des Maxillare als flaches Blättchen wulstartig mit der Hautbedeckung ventral vom Auge vor.

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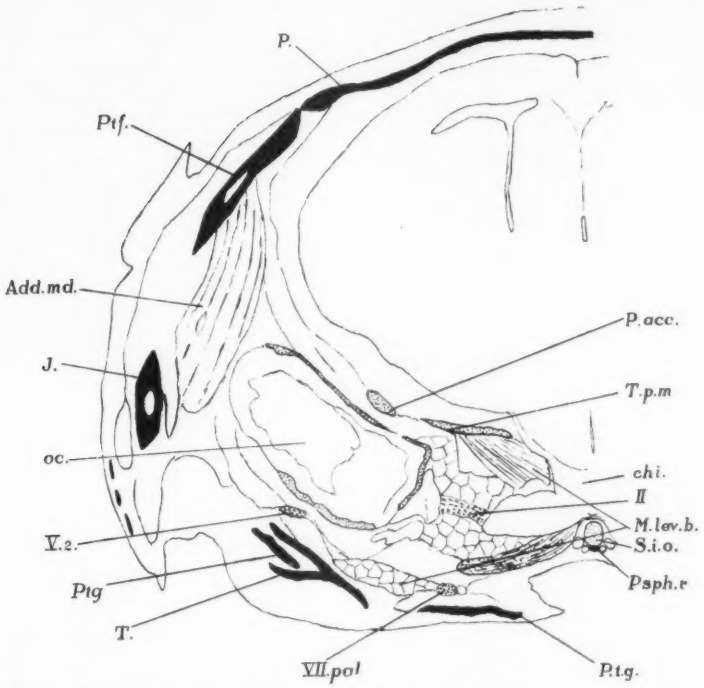

Fig. 15. Das Caudalende des Bulbus oculi ist getroffen. Das Jugale wächst dem absteigenden Ast des Postfrontale entgegen. Chiasma optici. Der Schnitt liegt knapp vor der Vereinigung der Pila accessoria mit der Pila metoptica, die kurz nachher die Pila antotica abgibt.

Hinter der Vereinigung der Commissura sphenethmoidalis mit dem hier kompletten Septum interorbitale tritt eine neue, grössere Durchbrechung des Septums auf, die im Bereich des stärksten Orbitaldurchmessers ein der Hirnbasis anliegendes Knorpelbälkchen (Rest des Planum supraseptale) von dem kurzen Septum interorbitale sensu stricto scheidet (Fig. 12).

An das Maxillare und Lacrymale schliessen sich von aussen das Jugale, von innen das Transversum an. Die Begrenzung des Gaumenfensters ist normal. Das Pterygoid, das den caudalen Abschluss des Knochenfensters bildet, fängt mit zwei Zipfeln an, einen medialen, der von aussen anfangs durch das Palatinum, und einen lateralen, der von innen her durch das Transversum umfalzt wird (Fig. 15). Im caudalen Bereich der Orbita schliesst an den vorher seitlich stark verdickten Rand des Frontale das Postfrontale an, das zum oberen Caudalabschluss der Orbita stark nach abwärts wächst; es erreicht aber nicht das ihm genäherte Jugale, so dass der Bogen nur unvollständig bleibt (Fig. 15 zeigt fast das Maximum der Vereinigung). Im Bereich der stärksten Orbitalausdehnung erweitert sich der schmale Supraseptalbalken zu einem Planum supraseptale, das bis zu den freien

Rändern des Frontale hinaufreicht; diese Seitenteile fangen schon hart am Frontalrand vor der Vereinigung zu einer vollständigen Schale an. Das Planum bleibt ca. 250 μ weit komplett (Fig. 14), verschmälert sich dann von oben her zu einer Rinne an der Hirnbasis (alles noch im Bereiche des Bulbus); im schmälsten Abschnitt ist ein unbedeutender medianer Durchbruch ausgespart.

Dem GAUPPschen Modell entsprechend folgt auf die Fenestra septi unter dem Septum supraseptale ein aufsteigender Ast des Interorbitalseptums, der in eine zweite Lücke der Septum supraseptale hineinragt, worauf der N. opticus aus der breiten Fenestra optica hervortritt. Im Beginn der Fenestra optica, die von der Taenia parietalis media (Pila metoptica) lateral und caudal, von der nur wenig tiefer liegenden Septalplatte ventromedial begrenzt wird, zieht jederseits ein isoliert beginnender Fortsatz, vom Rand des Postfrontale—Frontale beginnend, abwärts und vereinigt sich mit der Taenia parietalis medialis, die Pila accessoria (Fig. 15). Alle diese Knorpelbalken sind fast in einer Ebene ausgebreitet, das Septum interorbitale ebenfalls nur ein runder Stab, wenig unter dem Niveau des Opticusaustrittes. Der erwähnte Teil, die Pila accessoria, hat allerdings, verglichen mit dem GAUPPschen Modell, den primären Zusammenhang nach vorne verloren, da in diesem Bereich die Taenia marginalis fehlt; es handelt sich demnach nur um den caudalen, mit der Pila metoptica verbundenen Rest.

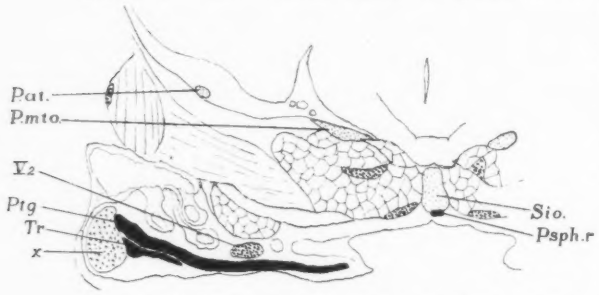

Fig. 16. Die Pila metoptica gibt die Pila antotica lateralwärts ab; x = fibröses Polster an der Gleitecke des Transversum und Palatinum gegen das Coronoid.

Im Gebiet der Fenestra optica beginnt das Rostrum des Parasphenoids an der Unterseite des Septum interorbitale. Der den caudalen Rand der Fenestra bildende Knorpelrahmen verbreitert sich nach Aufnahme der Pila accessoria neuerdings und gibt noch vor dem Verschluss des Fensters nach latero-caudal blind endigende, ganz zarte Bälkchen ab, die, den Hirnseiten angelagert, bis in das Niveau des Processus basipterygoideus reichen; es handelt sich um die Reste der Pila antotica (Fig. 16, 17). Der Endteil der caudalen Umgrenzung der Fenestra endet knapp ober dem Septum, ohne mit ihm zu verschmelzen; dieses zieht also unverändert durch das ganze Orbitalgebiet mit dem zarten Knochenblättchen des Processus cultriformis an der Unterkante.

Das alte Tier zeigt in dieser Region alle Differenzierungen des Chondrokraniums in gleicher Ausbildung, doch sind durch verschiedene Wachstums-

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verschiebungen die Relationen zu den umgebenden Dechknochen etwas verändert. Es lässt sich im allgemeinen feststellen, dass die Verschmälerung im Septalbereich noch stärker ausgeprägt ist, vor allem die Verengerung des Hirns zwischen Bulbus olfactorius und Hemisphären, so dass z. B. im Gebiet des Bulbusendes beim adulten Tier Tractusteile, beim jungen Tier aber die Hemisphären, ja auch Mittelhirnabschnitte mit dem Chiasma getroffen sind. So ist auch der Bereich des kompletten Septum supraseptale bis hinter das Auge vollständig und das Chiasma weit hinter dem Bulbus gelegen. Das Septum supraseptale ist dem Jungtier gegenüber reduziert, vor allem ist der vordere Seitenrand in eine zarte Spitze ausgezogen, die sich dann mit dem Ventralteil vereinigt; doch wird schliesslich auch hier vorübergehend das ganze Hirn im Bereich der grössten Orbitalbreite bis zum Schädeldach hinauf umspannt, während ventral zwischen Septum interorbitale und supraseptale ein grosser Durchbruch auftritt. Von einer Taenia marginalis ist natürlich auch hier keine Spur zu finden, die Pila accessoria ist erhalten (vielleicht entspricht doch ihr stark rostralwärts gerichteter Beginn einem Rest der T. marginalis). Am Beginn der Fenestra optica tritt eine Perforation auf, deren obere Umgrenzung, also eine Abspaltung des Interorbitalseptums, sich mit dem schmalen Septum supraseptale vereinigt (beim Jungtier fanden wir dagegen keine Verbindung und gleich das Auseinandertreten zum Foramen opticum). Der Rahmen des Fensters ist caudal überaus dünn. Der Verschluss erfolgt erst hinter der Einmündung der Pila accessoria und der Pila antotica; diese zieht samt dem Septum über den Bereich der Orbita weiter caudalwärts. Im ganzen sind

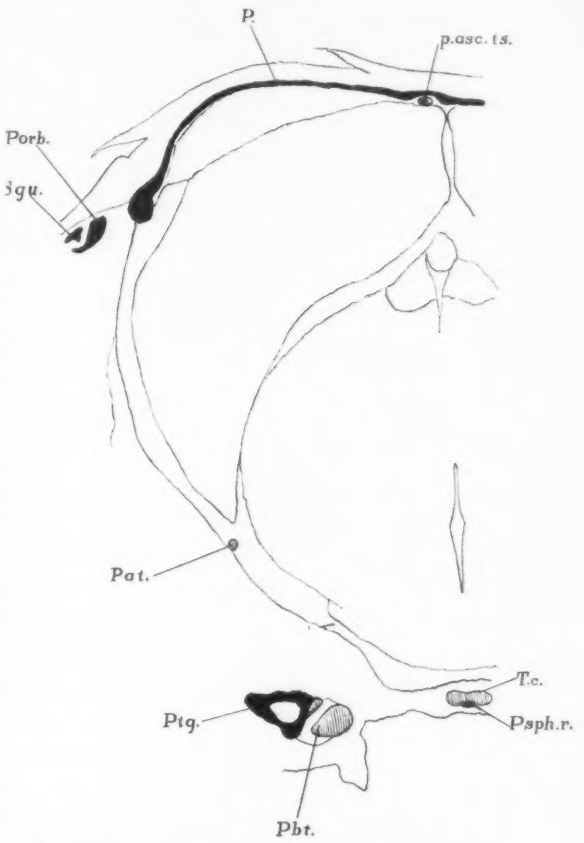

Fig. 17. Der rostrale Rest des Processus ascendens tecti synotici hinter dem Foramen parietale. Die Schläfenspange in ihrer grössten Entfernung von Parietale. Vorderster Teil des Basipterygoidgelenkes. Die Trabeculae cranii beginnen sich zu trennen.

also auch in dieser komplizierten Region die Unterschiede minimal bis auf die erwähnte Brücke zwischen Interorbitalseptum und Supraseptalseptum. Die Menge des Knorpels ist reduziert, die Spangen dünner, aber doch alle erhalten geblieben.

Nur beim jungen Tier liegt knapp hinter dem Parietalforamen, aber von ihm deutlich getrennt, im Parietale in der Höhe des vorderen Teiles des Basipterygoidgelenkes ein ca. 20 μ langer, runder Knorpelpfropfen (Fig. 17) in einer winzigen Perforation dieses Knochens. Offenbar handelt es sich um

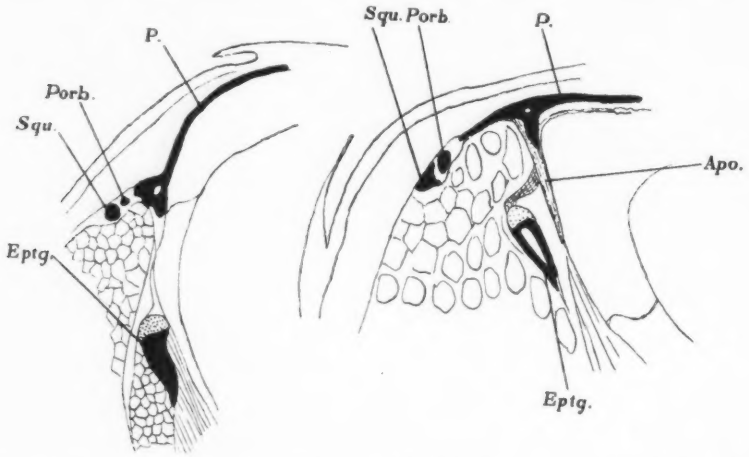

Fig. 18—19. Das obere Ende des Epipterygoids bei dem jüngeren (links) und dem adulten Tier (rechts); man beachte die Andeutung des Descensus parietalis und seine Verlängerung zu einer aponeurotischen Platte.

einen ganz ungewöhnlich weit vorgeschobenen Rest des Processus ascendens tecti synotici, der sonst, auch bei unserem Objekt, erst viel weiter caudal erhalten bleibt.

Nun sollen die Knochen der Schädelbasis behandelt werden, ferner das Epipterygoid. Das Gebiet des Basipterygoidgelenkes zeigt auch beim jungen Tier nur ganz minimale Reste eines Processus pterygoideus als vorderes Rudiment des Palatoquadratum; ca. 40—50 μ weit lässt sich in einer dorsalen Rinne des Pterygoids noch vor dem Gelenk ein isoliertes Knorpelbälkchen verfolgen, das aber mit dem Gelenkknorpel nicht kontinuierlich verbunden ist. Dieser (Fig. 17) beginnt an der dorsomedianen Ecke des Pterygoids, bleibt aber nur klein und breitet sich von der Oberkante des Knochens nicht über die Gelenkfläche aus. In der Pfanne für das Epipterygoid ist kein Knorpel vorhanden, wohl aber reichlich an beiden Enden dieses Knochens erhalten.

Beim Jungtier endet der Dorsalkopf an der membranösen Seitenwand des Schädels, das Parietale ist nur eine das Schädeldach bedeckende Platte.

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Beim alten Exemplar biegt von der Platte ein kurzer Descensus parietalis nach unten, der sich in eine Aponeurose fortsetzt; an dieser vorbei reicht der Dorsalkopf nach oben und heftet sich vom Perichondrium aus an sie. (Fig. 18, 19.)

An der Schädelbasis erhält sich Knorpel an den weit vorgeschobenen Gelenkfazetten der Processus basales des Sphenoids, die erst nahe der Schädelbasis verknöchern. Während diese medialwärts konvergieren, hört das Parasphenoidrostrum auf; die sich verbreitende Trabekelplatte zerfällt in zwei Bälkchen, die von den seitlichen Knochenflügeln umwachsen werden und verknöchernd sich zur einheitlichen Basalplatte schliessen. Wesentlich ist, dass das Parasphenoid nur als schmale ventrale Knochengräte ohne Schildteil entwickelt ist und eine deutliche Lücke zwischen seinem Caudalende und den sich um die Trabekel vereinigenden Basalfortsätzen bleibt. Beim alten Tier fehlt dieser Zwischenraum; das caudalwärts sich verbreiternde Parasphenoid geht allmählich in die ossifizierenden Trabekel über. Von da an ist schon beim Jungtier die Schädelbasis geschlossen und die Hypophysis in eine tiefe Fossa eingelassen. In diesem Bereich zieht die A. carotis interna durch ein seitliches Foramen in die Schädelhöhle.

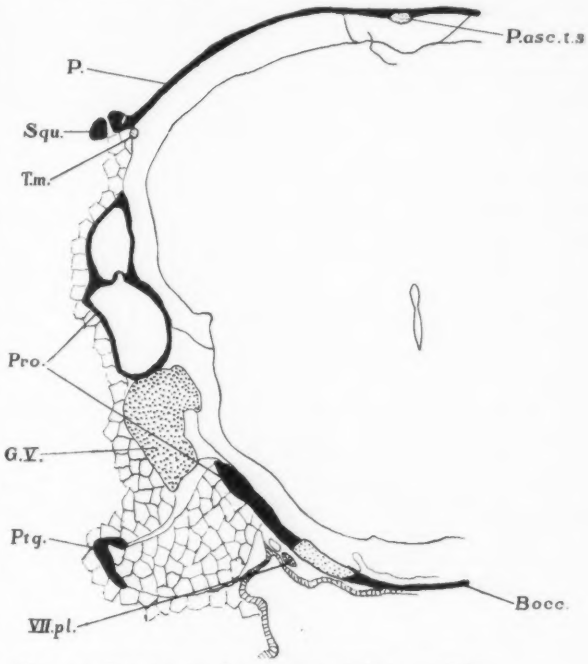

Fig. 20. Der bis in das Supraoccipitale verfolgbare Teil des Processus ascendens tecti synotici. Am freien Rand des Parietale der Rest der Taenia marginalis. Das Ganglion Gasseri liegt in einer Nische des Prooticum.

Unter das Trigeminusganglion schiebt sich (Fig. 20) ein Rostralfortsatz des Prooticum, dessen vorderster Teil knorpelig bleibt. Hinter dem Ganglion bleiben die aneinanderschliessenden Prootica und das Basisphenoid durchgehend durch eine Synchondrosis getrennt, deren Breite stark wechselt; auch zwischen Supraoccipitale und Prooticum bleibt eine Knorpelfuge. Vollständig sind aber das Basioccipitale mit dem Sphenoideum und die Exoccipitalia mit dem Basioccipitale verschmolzen. Beim zweiten Tier verschmelzen die Supraoccipitalia mit den Otica und diese mit Basioccipitale und Basisphenoid zu einem einheitlichen Hinterhauptsring. Es ist auffallend, dass bei der ebenfalls

kleinen Typhlops braminus so weitgehende Verschmelzungen eintreten, während bei dem Riesen der Familie, T. punctatus, die Elemente deutlich gesondert bleiben. An Resten des Primordialkraniums bleiben caudale Teile der Taenia marginalis erhalten. Am ventralen Lateralrand des Parietale beginnen sie als dünner Knorpelstrang unvermittelt und lassen sich beim Jungtier bis in die noch knorpelige obere Ecke der Ohrkapsel verfolgen, mit der sie bloss auf einer Seite vollständig zusammenhängen, an der anderen war bereits eine kurze Unterbrechung knapp vor der Kapsel vorhanden. Beim adulten Tier reicht die Taenia aber direkt in den Beginn der Ohrkapsel hinein, in der sie sich, von Knochen umwachsen, ein Stück weit verfolgen lässt. Es scheinen demnach geringe Schwankungen im Resorptionsprozess vorzuliegen (vgl. Fig. 20).

Der Processus ascendens tecti synotici beginnt, vom bereits erwähnten rostralen Rudiment abgesehen, im Bereich der grössten Breite des Os Parietale; der runde Knorpelstab zieht durch die über 200 μ lange Fontanelle zwischen dem caudalen Parietalrand und dem Supraoccipitale und wird dann von den sich median vereinigenden Supraoccipitalflügeln umwachsen, wo er sich bald verliert. Beim adulten Tier umgibt im Gegensatz hiezu ein vorgeschobener medianer Knochenmantel des Supraoccipitale sein Ende; dies zeigt, dass medial die Verknöcherung des Supraoccipitale craniad postembryonal fortschreitet, also die Tendenz besteht, die Fontanelle zu überbauen.

Der Jochbogen ist stark reduziert; die Postorbitalspange besteht im oberen Teil aus dem Postfrontale, das sich dahinter stark verschmälert und sich im Endabschnitt zur Bildung des überaus schmalen Temporalfensters unbedeutend vom Parietale entfernt. Gleichzeitig treten an dieses von aussen das Squamosum und als Zwischenstück das Postorbitale hinzu; hinter dem Postfrontale grenzt das Postorbitale an das Parietale, lateral vom Squamosum begleitet. Schliesslich grenzt durch ein beträchtliches Stück nur das Squamosum an das Parietale, dessen Caudalflügel seitlich weit ausladen (Fig. 2_1). Ein Schläfenfenster ist also kaum angedeutet (Fig. 17); es liegt zwischen dem etwas verdickten Seitenrand des Parietale und dem Innenrand des Postfrontale und Postorbitale, das aber im Endabschnitt wieder unmittelbar an das Parietale grenzt. Die eng aneinandergeschlossenen Caudalflügel des Parietale und Squamosum liegen schliesslich über den seitlich weiter vorragenden Ohrkapseln und legen sich caudalwärts immer mehr an diese an; schon vorher schaltet sich zwischen beide Knochen das Supratemporale (Fig. 21, rechts, 22). Im Bereich des Quadratum biegt das Squamosum nach unten — wie bei Chalcides guentheri — und dellt dessen knorpeligen Oberteil etwas ein, ohne dass es zu einer Foramenbildung kommt; beim adulten Tier war nicht einmal eine Eindellung vorhanden. Es kommt also nur in ganz annähernd angedeuteter Form zu der eigenartigen Doppelarti-

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kulation des Jochbogenendes, die manche andere Skinkiden besitzen. Knapp dahinter (Fig. 22) lagert sich das Supratemporale als Mantel um die noch unverknöcherte Labyrinthkapsel, die es ca. 100 μ lang, tief nach ventral herumbiegend, umkleidet, während das Parietale bis knapp davor zu verfolgen ist. Beim grossen Exemplar bleiben nach Ventralausbiegung des

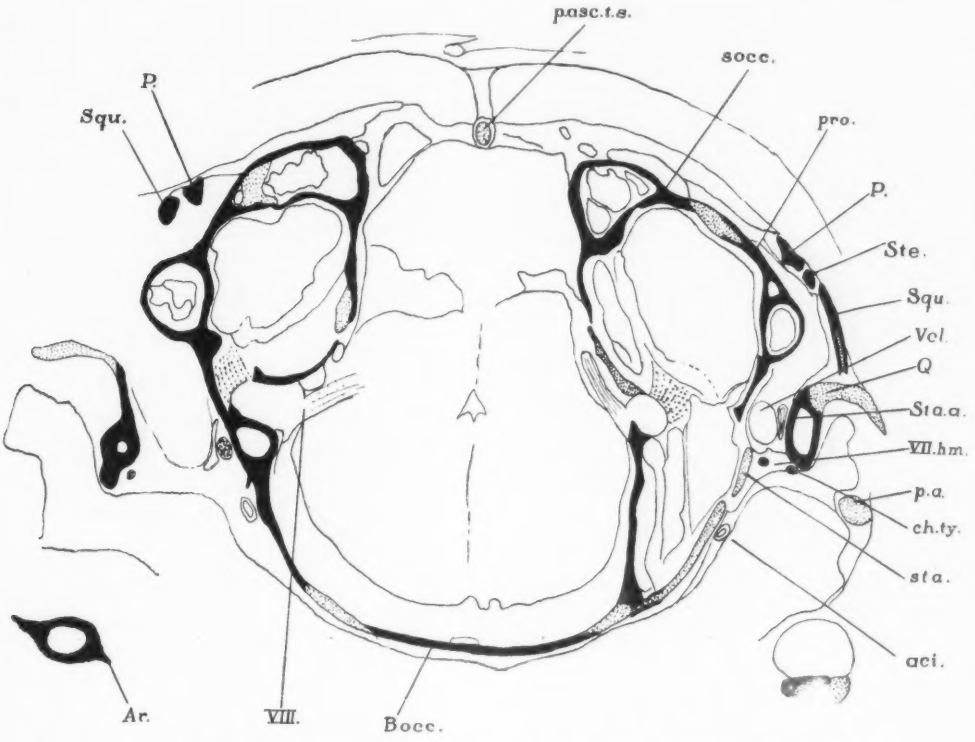

Fig. 21. Links knapp vor und rechts am Vorderrand des Foramen ovale. Rechts ist der Knorpelrand der Stapesplatte getroffen. Man sieht den knorpeligen Aussenrand des Quadratum und das Herausbiegen des Squamosum aus dem Bereich der Knochenspange, in der es sonst liegt. Beachte die typische Relation der Nerven und Blutgefässe zum Stiel der Columella.

Squamosum das Parietale und das Supratemporale dem Labyrinth eng angeschlossen, das Parietale reicht aber etwas weiter als das ventral auswachsende Supratemporale nach hinten.

Am Ventralende des Supratemporale (Fig. 22), deutlich vom Labyrinthknorpel getrennt (beim adulten Stück in diesem Gebiet bereits Verknöcherungen), liegt der Intercalarknorpel, der nicht mit Hyoidteilen zusammenhängt und caudal die Ohrkapsel umwächst.

Die Verknöcherung der Kapsel ist beim Jungtier noch recht wenig vorgeschritten; so bleiben nicht nur deutliche Knorpelbezirke dorsal gegen das

Supraoccipitale zu erhalten, sondern auch ventral gegen die Elemente der Schädelbasis hin. Der vorderste Teil der Ohrkapsel ist bei Juvenis vollständig verknöchert (im Gebiet des Ganglion V). Bei Adult. schliesst an diesen hohlen Anfangsteil eine vertikale Platte fast bis zum Schädeldach an und umgibt ihn auch cranial; in den oberen Rand dieser Lamelle, die etwas medial vom Aussenrand des Parietale endet, zieht die Taenia marginalis. Die Wachstums-

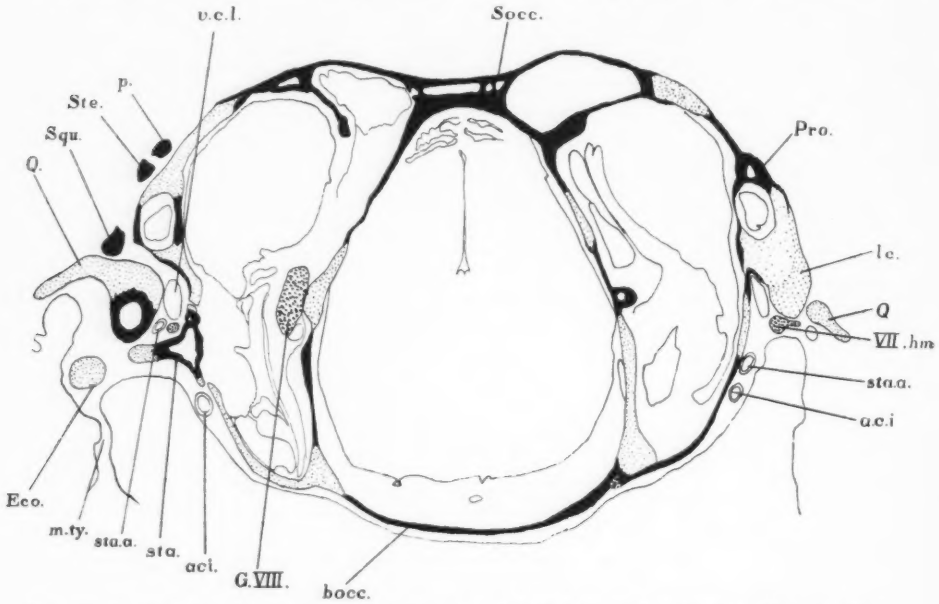

Fig. 22. Rechts: das Supratemporale umwächst die hier knorpelige Labyrinthkapsel. Der Processus posterior der Extracolumella ist ligamentös an das Quadratum geheftet; es fehlt der Processus internus.

verschiebung ist recht erheblich und dürfte in einer Verkürzung der Taenia von caudal her bestehen, denn bei juv. fehlt die flache Randleiste des Prooticum gängzlich und die Taenia endet erst dort, wo der knorpelige Oberrand der Labyrinthkapsel ihr Niveau erreicht, d. h. fast in der Höhe des Schädeldaches.

Beim Jungtier erhalten sich grössere Knorpelbezirke in der Umgebung des Supratemporale und caudal von diesem, dann in der Umgebung des Foramen ovale; dort bleibt eine breite Knorpelplatte zwischen Prooticum und Basioccipitale erhalten (Fig. 23). Die Region fällt durch ein starkes Ventralwachstum des Supraoccipitale auf, das die obere Hälfte der Ohrkapsel gegen die Hirnhöhle abgrenzt, während die untere teilweise knorpelig und im Zusammenhang mit der Synchondrosis basioccipito-prooticalis bleibt. Hinter dem Supraoccipitale ist die Verknöcherung wieder vollständig. Von diesen Knorpelresten ist beim adulten Tier kaum etwas zu bemerken; nur

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ventral an der früheren Lücke zwischen Basioccipitale und Prooticum erhalten sich von Knochen rings umgebene kleine Knorpelherde ventral vom Foramen ovale. Hinter dem Supratemporale, wo sich das Intercalare an die Kapsel anlagert, ist die Verknöcherung abgeschlossen bis auf einen kleinen Streifen unmittelbar unter dem Intercalare.

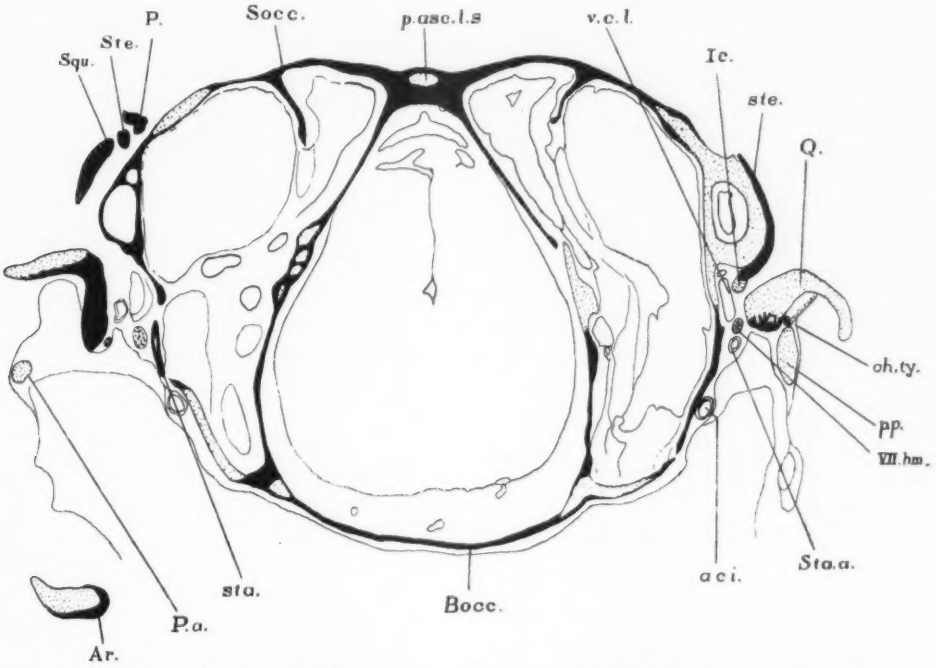

Fig. 23. Rechts: der Intercalarknorpel umwächst den Labyrinthknorpel; Abzweigung der Chorda tympani vom Ramus hyomandibularis des Facialis. Links Stapes und grösste Ventralerstreckung des Squamosum.

Der nierenförmige Condylus erhält nur beim Jungtier durch Knorpelfugen seinen zusammengesetzten Aufbau, später ist die Verschmelzung so vollständig, dass sogar die früher getrennten Markhöhlen zusammengeflossen sind; erst vor dem Condylus sind die bereits erwähnten kleinen Knorpelherde an der alten Synchondrosis stellenweise noch vorhanden.

Der Stiel und Ventralteil des Quadratum ist schon beim Jungtier weitgehend verknöchert. Der mit einem nach aussen gewölbten Überbau versehene Caudalfortsatz bleibt am äusseren Rand knorpelig und ist es caudal vom Stapelstiel durchwegs (bei beiden Tieren). Das hinter dem Basi-Pterygoidgelenk im Querschnitt rinnen-, dann plattenförmige Pterygoid endet ligamentös, dem unteren Quadratkopf angelagert.

Der Rand des Foramen ovale behält auch bei Adult. einen schmalen Knorpelsaum. Der Stapes trägt am Ende der knorpeligen kurzen Extra-

columella einen auffallend langen (260 μ) Processus anterior und einen viel kürzeren P. posterior (90 μ), der nach der Abzweigung in der Vertikalen nach oben biegt und als dünner Fortsatz am caudalen Tympanalrand endet. Der kurze Stabteil der Extracolumella geht nach einer ventrocaudalen Ausbiegung mit syndesmotischer Unterbrechung (Rudiment des Gelenkes) in die längere Columella über, deren Stiel und Platte verknöchern bis auf das distale Ende und den Plattenrand. Die Relation der Nerven und Blutgefässe zum Stapes ist normal, ebenso die Membrana tympani secundaria (Fig. 24).

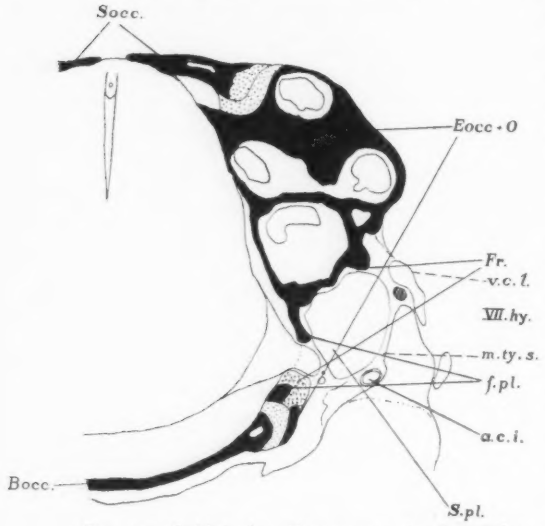

Fig. 24. Gebiet des Foramen rotundum, des Recessus scalae tympani. Man sieht die Membrana tympani secundaria. Die Kommunikation zwischen Sacculus perilymphaticus und den cranialen Lymphräumen liess sich an dieser Serie nicht in erwünschter Deutlichkeit zeigen.

Am Unterkiefer sind alle normalen Teile entwickelt: Dentale (bezahnt), Coronoid, Spleniale, Präarticulare, Angulare, Supraangulare. Das autostotische Articulare bildet nur den Postglenoidalfortsatz und ist mit dem Präarticulare verwachsen. Der Mekkelsche Knorpel persistiert im ganzen Kiefer, liegt im vordersten Bereich des Dentale median frei, ist aber dann allseitig von den Deckknochen umschlossen bis auf ein kurzes Stück in der Umgebung des Eintrittes von V. 3 in den Unterkiefer. Schon beim Jungtier zeigt der Knorpel kurz vor dieser Stelle histologische Umformungen, die auf eine von peripher einsetzende Verknöcherung hindeuten; ein schmaler Strang normalen Knorpels läuft aber ohne Unterbrechung zentral durch. Im Gelenkbereich liegen dem kompakten Knorpel das Supraangulare und Präarticulare als dünne Blättchen auf; erst unterhalb vom caudalen Gelenksabschnitt erfolgt der allmähliche Übergang zum Ersatzknochen. Beim alten Tier ist in der Region vor dem Epipterygoid der Meckelsche Knorpel atrophiert, in das Perichondrium ein Blutgefäss eingedrungen, das den Knorpel von vorn nach hinten gänzlich verdrängt. Das Supraangulare und Präarticulare verschmelzen fast gänzlich und mit dem im alten Lumen noch als solches an der Lamellenanordnung erkennbaren verknöcherten Perichondriumrohr. Anstelle der grossen Knorpelmasse vor und im Gelenk tritt im einheitlichen Knochen („Grossknochen" LAKJERS) ein System von Markräumen auf; der Gelenksknorpel ist nur auf einen verhältnismässig dünnen Belag der Fazette beschränkt. Das Articulare wächst also postembryonal

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stark cranialwärts bis vor die Gelenksregion anstelle des früheren Knorpels weiter und verschmilzt dann mit dem Perichondrium und den beiden caudalen Belegknochen. In der rostralen Kieferregion treten keine nennenswerten Unterschiede auf.

Im allgemeinen lässt sich sagen, dass an vielen Stellen des Schädels beim adulten Tier die Muskelvorsprünge wesentlich stärker hevortreten als beim jungen, sogar ganz neu erst auftreten, wie am Unterkiefer, am Pterygoid (caudal, besonders an der Basis cranii). Im einzelnen wurde auf diese meist nur graduellen Unterschiede nicht näher eingegangen.

Zusammenfassend liesse sich über diesen Schädel etwa folgendes hervorheben. Der embryonale Knorpelschädel bleibt bis in das adulte Stadium weitgehend erhalten bis auf den starken Abbau des Knorpels in der Regio otica zugunsten der Ersatzknochen, die sich nicht nur an Stelle des embryonalen Knorpels ausbreiten, sondern auch ein starkes peripheres Wachstum zeigen, das zur Bildung von Randplatten und Muskelvorsprüngen führt (Prooticum, Exoccipitale); mit diesem Prozess geht eine Verschmelzung der caudalen Knochen Hand in Hand. Verglichen mit einem vollständigen Lacertilier-Chondrocranium erscheint nur der vordere Teil der Taenia marginalis reduziert, ferner der caudale Anschluss der Pila antotica an die Labyrinthkapsel. Reduziert sind ferner stark der Processus maxillaris der Ethmoidkapsel und der Processus pterygoideus vor dem Epipterygoid. Auch ist die dorso-laterale Nasenkapselwand durch Vereinigung der lateralen Nasenfenster weniger vollständig. Auffallend ist beim Jungtier der weit vorn im Parietale gelegene Knorpelpfropfen, wohl ein isolierter, vorgeschobener Rest des erst viel weiter caudal kontinuierlichen Processus ascendens tecti synotici. Der adulte Schädel zeigt ausser der Verschmelzung der Autostosen des Hinterhauptes Synostosis der drei caudalen Unterkieferknochen. Erst bei diesem Schädel war das Parasphenoid mit dem Basiphenoid verwachsen. Ganz spät verknöchert das Supraorbitale. Während des Wachstums steigert sich der tropibasische Bau des Schädels durch Verschmälerung der Interorbitalregion, der Tractus olfactorius bildet sich erst spät zu einer schmalen Kommissur aus. Hieraus ergeben sich bedeutende relative Verschiebungen der Teile gegeneinander im Orbitalgebiet. Der Bau des Schädels lässt auf eine grosse Bedeutung der metakinetischen Beugungslinie zwischen dem otischen Segment und dem Parietale schlissen, da die zwischen beiden bleibende grosse Lücke weitgehende Bewegungen zulassen muss. Andererseits spricht die Aufhebung einer starren Postorbitalverbindung für kompliziertere intrakranielle Bewegungen, auch die wohlausgebildeten Gelenke an beiden Epipterygoidenden; es wird demnach ein Intermediärtypus zwischen dem meso- und metakinetischen Zustand vorliegen.

Bemerkenswert ist auch neben der schwachen Entwicklung der caudalen Elemente des Gaumenskelettes und dem Mangel der Bezahnung an diesen

die Atrophie des Jochbogens, der zwar in allen Teilen erhalten bleibt, aber praktisch funktionslos sein muss. Das Schläfenfenster ist zu einem winzigen Spalt reduziert und der verdickte Aussenrand des Parietale zum einzigen verstärken Teil der Temporalregion geworden. Die Elemente, die den Bogen bilden, bleiben eine längere Strecke an das Parietale direkt angeschlossen als von ihm zur Fensterbildung entfernt. Die Aufhebung der Postorbitalspange ist wohl die Voraussetzung der Jochbogenatrophie und wohl ganz typisch für den bei den Reptilien nicht seltenen Prozess des restlosen Schwundes der Schläfenbogen.

VERZEICHNIS DER ABKÜRZUNGEN.

aci. Arteria carotis interna.
Add. md. Adductor mandibulae.
Apo. Aponeurose.
Ar. Articulare.
Bocc. Basioccipitale.
cc. Conchalknorpel.
cec. Cartilago ectochoanalis.
chi. Chiasma optici.
ch. ty. Chorda tympani.
C. n. Cavum nasi.
c. o. J. Knorpelkapsel des Jacobsonschen Organes.
covn. Concha des Org. vomero-nasale.
c. ps. Cartilago paraseptalis.
c. seth. Cartilago sphenethmoidalis.
dnl. Ductus naso-lacrymalis.
Eco. Extracolumella.
Eocc. + *O.* Exoccipitale + Prooticum.
Eptg. Epipterygoid.
F. Frontale.
fen. d. n. Fenestra dorsalis (+ lateralis) nasi.
f. pl. Foramen perilymphaticum.
F. so. fibröse Anlage des Supraorbitale.
f. r. Fenestra rotunda.
G. Ganglion.
gl. H. Glandula Harderiana.
gl. n. Glandula nasalis.
hy. VII. Ramus hyomandibularis Facialis.
Ic. Intercalare.
J. Jugale.
La. Lacrymale.
M. lev. b. Musculus levator bulbi.
mty. Membrana tympani.
m. ty. s. Membrana tympani secundaria.
N. Nasale.
na. Naris.
nc. Nasenkapsel.
oc. Bulbus oculi.
ovn. Organon vomero-nasale.
P. Parietale.
p. a. Processus anterior extracolumellae.
Pal. Palatinum.
P. asc. t. sy. Processus ascendens tecti synotici.
pbt. Processus basitrabecularis.
Pf. Präfrontale.
pl. at. Planum antorbitale.
pl. VII. Ramus palatinus facialis.
P. at. Pila antotica.
P. mto. Pila metoptica.
Pmx. Prämaxillare.
P. mx. Processus maxillaris der Nasenkapsel.
Porb. Postorbitale.
p. p. Processus posterior extracolumellae.
Pro. Prooticum.
Psph. r. Parasphenoidrostrum.
Ptf. Postfrontale.
Ptg. Pterygoid.
Pv. Prävomer.
Q. Quadratum.
rln. Ramus lateralis nasi.
rmn. Ramus medialis nasi.
sio. Septum interorbitale.
Smx. Supramaxillare.
sn. Septum nasi.
Socc. Supraoccipitale.
Spl. Saccus perilymphaticus.
Spt. Septomaxillare.

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Sq. Knochenschuppen.
Squ. Squamosum.
s. s. Septum supraseptale.
Sta. Stapes.
sta. a. Arteria stapedialis.
Ste. Supratemporale.
T. c. Trabeculae cranii.
T. m. Taenia marginalis.
T. p. m. Taenia parietalis medialis.
Tr. Transversum.
vcl. Vena capitis lateralis.
zk. Zahnkeim.

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COMPARATIVE OBSERVATIONS ON HEAT CONTRACTURE AND EXCITABILITY AT VARIOUS TEMPERATURES IN SKELETAL MUSCLES OF COLD-BLOODED ANIMALS. I.

BY

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For poikilothermal animals, whose body temperature is dependent on the temperature of the surrounding medium, there exists to a certain extent an optimum temperature at which they grow and thrive best. In general this temperature is the normal temperature range of the environment to which the organism is acclimatized.

The aim of this investigation is to study comparatively the range of temperature at which heat contracture in excised skeletal muscles begins, reaches its maximum, and is completed and furthermore, to determine the temperatures at which the excitability by direct electric stimulation is highest (maximum tetanus), decreases, is last observed, and then disappears. The skeletal muscles were taken from various poikilothermal species, which naturally are living in surroundings whose mean temperatures differ. If the supposition is correct, that between the temperature-susceptibility of the skeletal muscles and the external ecological temperature conditions, under which the animals move, there exists a certain relation, then differences in that respect should be observed in muscles taken from species naturally living in surroundings of different mean temperatures and these differences should be correlated to a certain extent.

In the present paper results on the skeletal muscles of some species of fish are reported. The species used are:

2 Marine types[1]:	Conger eel (Conger vulgaris)
	Dogfish (Squalus acanthias)
4 Fresh water types:	Goldfish (Carassius auratus)
	Catfish (Ameiurus nebulosus)
	Sunfish (Eupomotis gibbosus)
	Carp (Cyprinus carpio)

Results on muscles from reptiles and amphibians living naturally in a warm or temperate climate will be reported in a subsequent publication.

The question of heat contracture and its irreversible endpoint—heat rigor—has been investigated extensively in skeletal muscles of frogs. Rana esculenta and Rana temporaria were usually used, Rana fusca less frequently (1 to 12). VERNON (3) observed that the first step of shortening due to temperature influences occurs at a temperature which is 2.7°C. at the onset and 4.7°C. at the culmination lower in the skeletal muscles of Rana temporaria than in those of Rana esculenta.[2] REISSNER (6) was able to confirm this results. Rana temporaria is found somewhat farther to the north than Rana esculenta, and it is the only European frog species which can be found at elevations as high as 6000 feet.

Very little literature from a comparative view point is available with respect to the loss of functional activity under various temperatures in the skeletal muscles of other cold-blooded animals. PATZL (13) extended her observations on skeletal muscles of Lacerta serpa, L. viridis, L. agilis and L. vivipara, in addition to Rana temporaria and Rana esculenta. In the muscles of Lacerta viridis, the heat contracture begins at 37—39°C., in those of Lacerta serpa at 41—43°C. Both species are living in a comparatively warm climate, Lacerta serpa farthest south (Mediterranean region). Heat contracture begins at 30—32°C. in the muscles of Lacerta vivipara, in those of Lacerta agilis at 34—36°C. Both species are living farther north, Lacerta vivipara particularly being found at higher regions above sea level than any other of the species investigated, (up to 9000 feet, where the external mean temperatures are far lower, particularly in the cold seasons).

There are only a few published experiments on heat contracture in fish muscles. Those by Vernon were on the muscles of the common small eel and goldfish, and the temperature was raised gradually but continuously. More recently BATTLE (14) has studied the twitches of muscles of skates, flounders and Myoxocephalus, lying in Petri dishes, the temperatures of which were gradually raised (direct stimulation, constant current).

[1] The experiments on these types were done in Woods Hole, Mass. Marine Biological Laboratory.

[2] Rana esculenta: 33.7—46.6°C.
Rana temporaria: 31.0—41.9°C.

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METHOD.

The muscles found to be best suited for study in the species of fish reported in this paper were straight parallel-fibered ones which insert at the lower jaw and end near the anterior fins.

After being carefully prepared the muscle was placed in a Dewar vessel which was filled with fresh Ringer solution. One end of the muscle was attached to the short arm of an L-shaped glass tube which was inserted through the large cork stopper, the other end was attached to the short arm of a light lever by means of a thread (previously boiled to prevent further shrinking). The stimulating electrodes were led through the L-shaped tube. In addition to this tube the cork stopper held an aeration tube and a sensitive thermometer, the latter being so adjusted that its bulb was close to the muscle. Aeration of the Ringer solution was carried out continuously during an experiment.

The temperature of the Ringer solution was raised in steps of 0.5—2.0°C. by exchanging the Dewar vessel for one prepared accordingly. *Stepwise change instead of gradual heating* proved far more satisfactory. No clear-cut results are obtained by gradually raising the temperature. The muscle was kept at least 5 minutes at any given temperature, longer when the maximum slow heat contracture occurred, in these instances till the muscle had reached the maximum shortening according to the particular temperature. WAGNER (15) showed, by thermoelectric measurement, that frog's gastrocnemius muscles reached the temperature of the surrounding fluid in one and a half minute. Up to 41—42°C. the temperature in the Dewar vessel is constant even during 5 minutes or longer. Beyond that, a few tenths of a degree decrease would occur after about 5 minutes. The stationary drum was turned by hand before each change. The shortenings of the muscle were registered isotonically, the load to be lifted by the muscle was adjusted to its size.

Starting at room temperature, the muscle was stimulated at each step by faradic current so as to produce a maximum tetanus. On account of the fact that a large proportion of the current is short circuited by the immersion of the electrodes in the Ringer solution, 3 dry cells were used in the primary circuit of the inductorium. The height of the tetanic contraction curve can be taken as the indicator of muscular exitability, if the strength of the stimulus is kept constant. In the present paper, the figures given represent the vertical distance in mm. from the top of each tetanus to the base line, the base line being uniformly a straight horizontal line in the regions of temperature before the onset of heat contracture.

The length of the muscle, when fixed for registration, was measured at the beginning of the experiment and at the end when the heat rigor was complete. At higher temperatures, in a number of cases, a slight lengthening again occurred, this lengthening being probably due to the muscle having lost elasticity after the culmination of the heat rigor so as to permit a stretch under the load. VERNON (3) observed the same phenomenon in frog's muscles up to 51°C. JENSEN (8), working on the sartorius muscle of Rana fusca, which reaches the maximum of heat contracture at 42°C., states, that between 42—50°C. the relaxation of the muscles is only very slight, in many cases almost negligible. Between 50—65°C., however, the muscle becomes increasingly extensible if the load is not too small.

CONGER EEL (*Conger vulgaris*).[1]

Twelve animals were investigated. See Tables 1 and 2 and Figure 1.

The muscles were given an average load of 40.1 g., ranging from 35—45 g. The heat contracture sets in and is completed within a range of 3.5°C. (average 35.0—38.5°C.), the muscle having decreased in length by an average of 32.2 %. From 38.5—44.0°C. the muscle length remains constant. In 8 out of 12 cases a slight lengthening began at 44°C., amounting to 1.5 mm. (on the record, average) or 1.2 % of the total heat contracture. At 48°C. this lengthening had reached 3.7 mm. (average) or 2.8 % of the completed heat contracture. Up to 52°C. no further lengthening occurred.

The excitability of the muscles decreases with increasing temperature and

Table 1.

Heat Contracture of Muscle—Conger Eel (12 animals).

Muscle length mm.	Before heat contracture		After completion of heat contracture		Decrease of muscle length	
	Average	Range	Average	Range	Average	Range
	59.2	50—65	40.1	30—46	32.2%	24—40%
Heat contracture.	Beginning of heat contracture.					
	Temperature		% of maximum heat contracture			
	Average	Range	Average		Range	
	35.0°C.	34.0—36.0°C.	12.3		0.8—60.7	
	Completion of heat contracture.					
	Temperature		Maximum heat contracture			
	Average	Range	Average		Range	
	38.5 C.	37.5—39.5°C.	130 mm.		99—158 mm.	
	Last temperature observed before beginning of heat contracture		Actual shortening of muscle in maximum heat contracture[2]			
	Average	Range	Average		Range	
	34.5°C.	33.5—36.5°C.	16.2 mm.		12.4—19.8 mm.	

[1] Subclass Teleostei. The Conger eel is a strictly marine, very active fish, preferring deep waters.

[2] Magnification uniformly 1:8; load fastened on the opposite side of the fulcrum at the same distance as the attachment of the muscle thread.

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Table 2.

Excitability (Conger Eel).
(Maximum tetanus, direct muscle stimulation, faradic current).

	(1)		(2)		(3)		(4)		(5)		(6)	
	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
Temperature °C.	22.5	18.1 — 25.8	25.5	23.5 — 27.5	28.5	24.5 — 30.5	30.5	29.0 — 33.3	32.7	30.5 — 34.0	33.7	32.5 — 35.0
Maximum tetanus mm.[1]	144	110 — 160	138	92 — 160	111	40 — 160	85	36 — 160	42	10 — 112	20	3 — 51
Percent of highest response in (1)	100		96		77		59		29		14	

$$\frac{\text{Maximum heat contracture}}{\text{Maximum tetanus (1)}} = \frac{130}{144} \text{ or } 90\%$$

[1] Actual shortening = values given, measured on the records, divided by 8 (Magnification 8×).

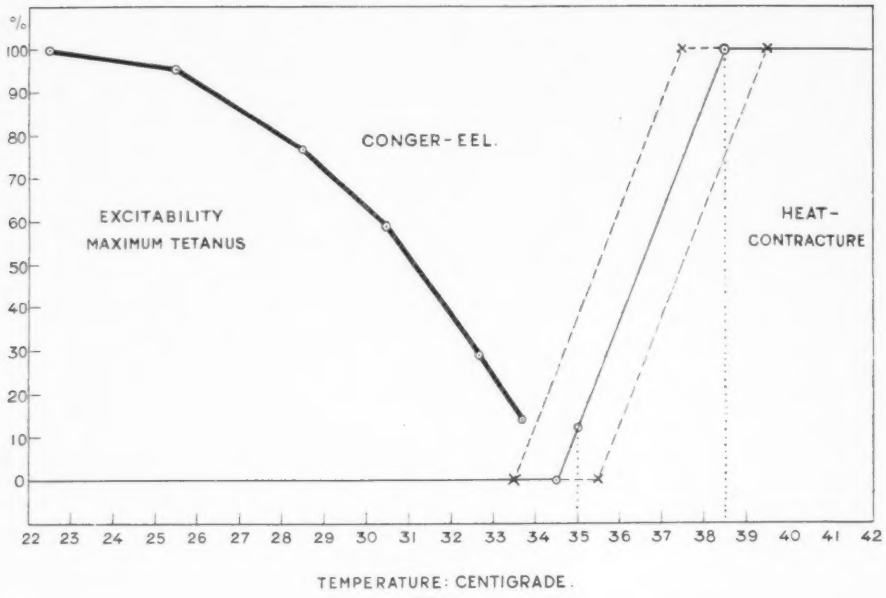

Fig. 1.

disappears entirely beyond 33.7°C., the average of the last responses observed was 14 % of the initial or highest responses. *Uniformly* the muscles are not excitable to direct stimulation shortly before the heat contracture begins (Fig. 1). The ordinate in Figure 1, and also in the following figures, represents percentages and refers to two sets of values. The maximum heat contracture as well as the maximum tetanic response is counted as 100 %.

The area between the dotted lines includes all heat contracture curves. The average curve is drawn in a full line within that area. Having reached the completion of the heat contracture, the shortening of the muscles had proceeded to a point which was 90 % of that obtained in the highest maximum tetanus (100 %). JENSEN (8) says that in muscles of Rana fusca the shortening in complete heat rigor at 44°C. is very near to their shortening in maximum electric tetanus. The range of temperatures between onset and completion of heat contracture is smaller in the muscles of the conger eel than in the muscles of frogs and lizards.[1]

[1] PATZL (13) finds the range between: 34—39°C. Rana temporaria.
37.5—43°C. Rana esculenta.
31—43°C. Lacerta vivipara.
35—45.5°C. Lacerta agilis.
38—46.5°C. Lacerta viridis.
42—46.5°C. Lacerta serpa.
The largest range, 12°C. is with Lacerta vivipara, being in nature exposed to widely differing temperatures at the various seasons as a mountain lizard. GOTTSCHLICH (1) finds that in the muscles of frogs caught in spring and having lived through the winter outside, heat contracture begins at a lower temperature than in muscles of frogs caught in the fall.

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According to PATZL (13), working with the same method as the one used in these investigations, the muscles of Rana temporaria are still excitable at 38°C., those of Rana esculenta at 41°C. and those of Lacerta serpa at 46°C. In the muscles of the conger eel, no excitability can be found beyond 35°C., the last responses recorded in some cases being at that temperature. PEREIRA (16) states that neither warming nor cooling increases the excitability of frog's muscles, but diminish it instead. The optimum temperature at which the excitability of frog's muscles is greatest is that at which the animal has been maintained before the experiment. The natural surroundings of the conger eel (cold ocean) are certainly more constant as far as the temperature is concerned than those of the previously mentioned land species—the mean temperature being far below the temperature at which the muscular exitability disappears irreversibly. The common eel, which decends to the ocean from the rivers at certain times for breeding purposes and which was investigated by VERNON (3), shows loss of excitability of its muscles at 39.2°C. (mean of 5 experiments). The range between onset and culmination of heat rigor was given as 28.5—44.6°C.

DOGFISH (*Squalus acanthias*).[1]

Fifteen animals were investigated. See Tables 3 and 4 and Figure 2. In the dogfish muscles, the range within which heat contracture starts and is completed is wider than in the conger eel muscles (6°C.) and heat contracture starts earlier, at 29°C. The decrease of muscle length is about the same in both species—30 % in heat rigor. The muscle length remained constant in all 15 cases, between 37—40°C.; in 7 of them it remained constant up to 50°C. In 8 cases a subsequent lengthening occurred. At 41.6°C. the record had fallen to 90 % of its maximum heat contracture level. The area between the dotted lines, including all heat contracture curves, is wider than in conger eel muscles, the variability being greater.

The last muscle response obtainable from direct electrical stimulation was observed at an average temperature of 31.6°C., the response being 17 % of the highest initial response. Battles (14) reports that the mean between the last temperature at which irritability is present and the lowest recorded temperature at which there is no response in the muscles is 31.6—28.3°C. for skates, 31.4—29.9°C. for flounders, and from 28.7—27.6°C. for Myocephalus decimspinosus. Another difference between the conger eel and the

[1] Class Elasmobranchii, subclass Selachii. (Skeleton cartilaginous.) In some respects this group is highly organized, while in others its members stand on a lower grade of development as the members of the class of Pisces.

Table 3.

Dogfish, 15 animals observed.

Muscle length mm.	Before heat contracture		After completion of heat contracture		Decrease of muscle length	
	Average	Range	Average	Range	Average	Range
	42.2	30—57	29.6	19—44	30%	6.7—52.5%
Heat contracture	Beginning of heat contracture.					
	Temperature, °C.		% of maximum heat contracture			
	Average	Range	Average		Range	
	29.0	25.5—32.5	17		0.8—44	
	Completion of heat contracture.					
	Temperature, °C.		Maximum heat contracture			
	Average	Range	Average		Range	
	35.0	33.0—37.0	102 mm.		17—171 mm.	
	Last temperature observed before beginning of heat contracture		Actual shortening of muscle in maximum heat contracture			
	Average	Range	Average		Range	
	27.8	24.0—31.5	12.7 mm.		2.1—21.4 mm.	

Magnification 8×. Load: Average 25.3 g.
Range 10—45 g.

Table 4.

Excitability (Dogfish).
(Maximum tetanus, direct muscle stimulation, faradic current).

	(1)		(2)		(3)		(4)	
	Average	Range	Average	Range	Average	Range	Average	Range
Temperature °C.	23.5	21.0—24.8	27.0	25.8—28.1	30.0	28.5—31.4	31.6	28.5—34.5
Maximum tetanus mm.[1]	69	10—139	62	7—105	43.4	6—93	11.8	1—52
% of highest response in (1)	100		90		63		17	

$$\frac{\text{Maximum heat contracture}}{\text{Maximum tetanus (1)}} = \frac{102}{69} \text{ or } 148\%$$

[1] Actual shortening = values given, measured on the records, divided by 8 (Magnification 8×).

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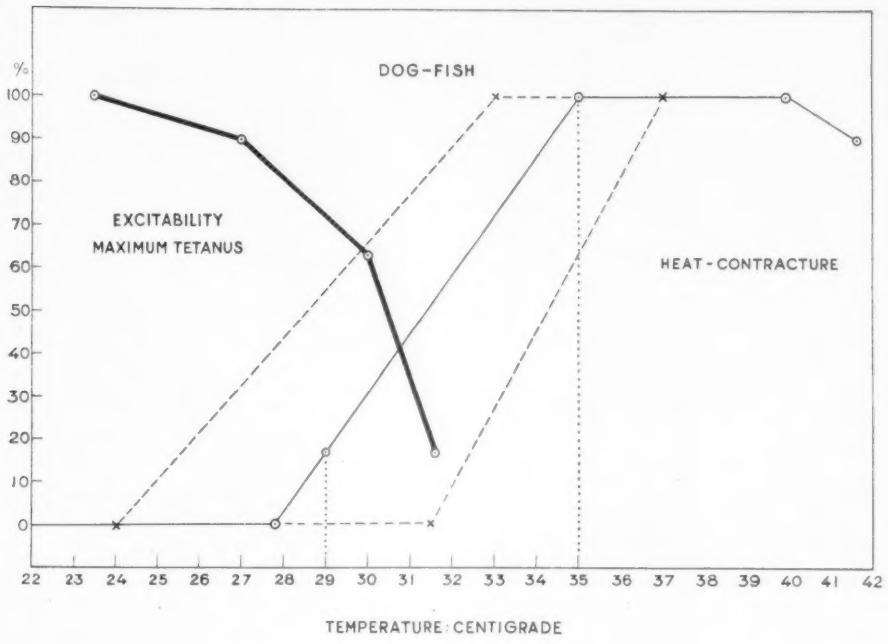

Fig. 2.

dogfish, the two marine species investigated, is that the average shortening of the muscles at the culmination of heat contracture is only 90 % of the maximum shortening of tetanus in the former while it is 148 % in the latter. Values higher than 100 % have not been observed in any of the other species of fish investigated.

GOLDFISH (*Carassius auratus*).[1]

Ten large goldfish were investigated; most of them had reverted to their natural greenish hue. See Tables 5 and 6 and Figure 3. In the goldfish the range of temperature at which heat contracture sets in and is completed is 2°C. (lower than in the muscles of the marine species). The muscles of this fresh water species decreased 13.5 % of their length in heat rigor, and the muscle length remained constant after completion of the heat contracture up to 42°C. Beyond this a slight extension occurred at 43.8°C. (average), at which temperature the record had fallen to 93 % and at 51°C. to 83 % of that of the muscle in full heat rigor.

[1] Subclass Teleostei, family Cyprinidae. For the most part the Cyprinidae are small and feeble fishes of comparatively simple structure, embracing less active species, bottom feeders, and forming a large share of the food of predatory fishes.

Table 5.

Goldfish, 10 animals observed.

Muscle length mm.	Before heat contracture		After completion of heat contracture		Decrease of muscle length	
	Average	Range	Average	Range	Average	Range
	24	21—27	21	18—24	13.5%	16.5%—8.7%
Heat contracture	Beginning of heat contracture.					
	Temperature, °C.		% of maximum heat contracture			
	Average	Range	Average		Range	
	37.0	35.5—38.5	27.0		9.7—81.0	
	Completion of heat contracture.					
	Temperature, °C.		Maximum heat contracture			
	Average	Range	Average		Range	
	39.0	38.0—40.0	24 mm.		14—34 mm.	
	Last temperature observed before beginning of heat contracture		Actual shortening of muscle in maximum heat contracture			
	Average	Range	Average		Range	
	36.3	34.6—37.9	3.0 mm.		1.75—4.25 mm.	

Magnification 8×. Load: Average 7.5 g.
Range 5—10 g.

In goldfish the exitability curve in relation to temperature has a different shape from the curves in conger eel and dogfish muscles. The last average temperature at which a tetanic response (11 % of the highest tetanic response on the average) is observed is 34°C. VERNON (3) finds that the loss of excitability in goldfish muscles occurs at 39.4°C. (5 experiments) and heat contracture occurs between 33.4—41.8°C. According to him the muscles of the common eel contain twice as much solids as those of the goldfish (15 %). The shortening of the muscles in complete heat rigor, 92.5 % of their shortening in highest maximum tetanus, is closely related to the value arrived at in conger eel muscles.

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Table 6.

Excitability (Goldfish).
(Maximum tetanus, direct muscle stimulation, faradic current.)

	(1)		(2)		(3)		(4)		(5)		(6)	
	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
Temperatur °C.	21.2	17.0—24.0	24.2	20.7—26.8	27.0	24.9—30.0	29.5	27.0—32.8	32.5	28.0—34.3	34.0	29.8—36.0
Maximum tetanus mm.[1]	26	8—54	16	4—32	10.4	2—26	6.5	2—20	3.9	1.5—7	2.8	1—5
% of highest response in (1)	100		61.5		40		25		15		11	

$$\frac{\text{Maximum heat contracture}}{\text{Maximum tetanus (1)}} = \frac{24}{26} \text{ or } 92.5\%$$

[1] Actual shortening = values given, measured on the records, divided by 8 (Magnification 8×).

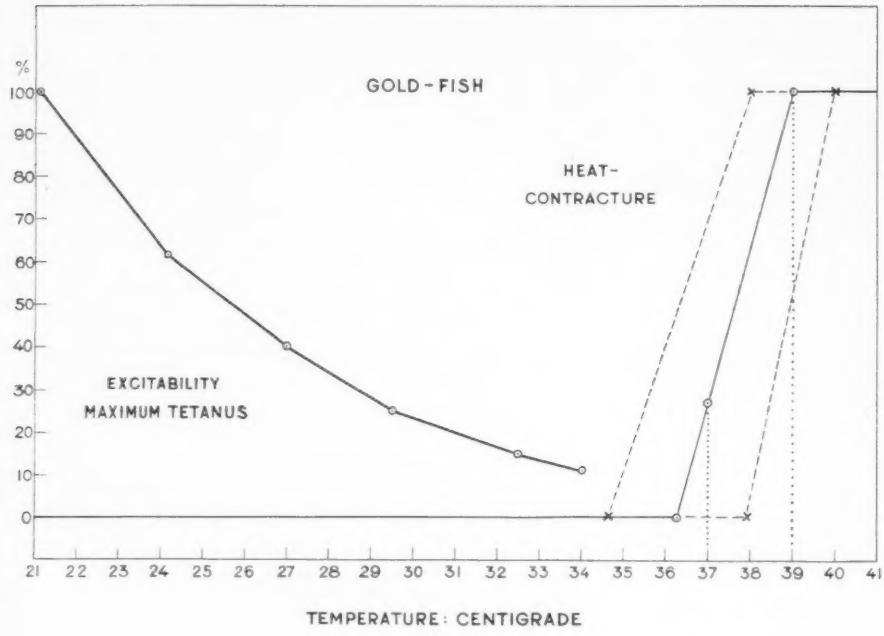

Fig. 3.

CATFISH (*Ameiurus nebulosus*).[1]

Ten animals, about 10—12 inches long were studied. See Tables 7 and 8 and Figure 4. The muscle length remains constant after completion of the heat contracture in most cases up to 50°C. The last (average) temperature in which a tetanic response (18.7 % of the highest response on the average) is observed is 30°C., *uniformly* shortly before the heat contracture begins. In full heat rigor the muscle length is 90 % of the shortening in maximum tetanus.

SUNFISH (*Eupomotis gibbosus*) and CARP (*Cyprinus carpio*).

Six sunfish and ten carp (1—2 pounds weight) were investigated. See Table 9 and Figure 5. The temperature range for heat contracture is wider in the sunfish (5°C.) than in the carp (3°C.). The muscle length remains practically constant after heat rigor is reached.

Discussion.

The body temperature of fish varies with the temperature of their environment and any attempt at heat regulation can in most of the species hardly be

[1] Absence of true scales. The catfish is a sluggish groundfish, growing best in weedy ponds and waters with little current. They can endure removal from water longer than any other fresh water fish.

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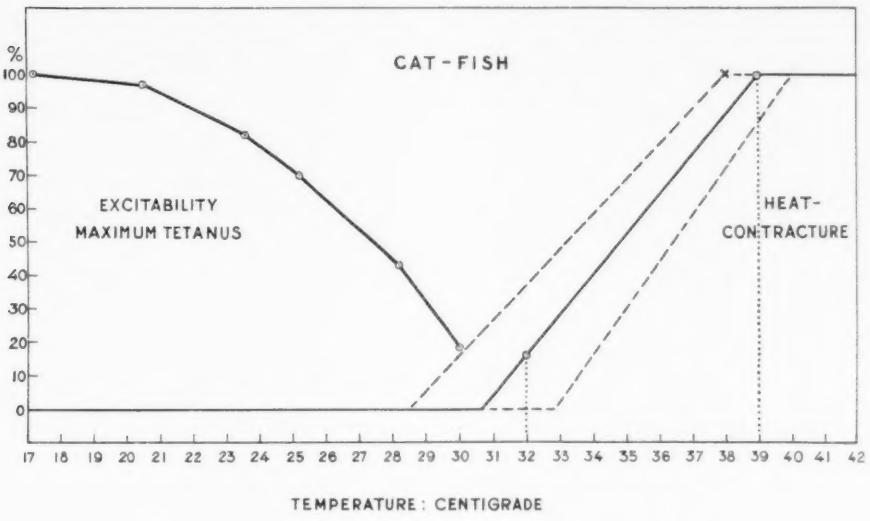

Fig. 4.

said to exist at all. The range of temperature at which different species of fish are living is very great, the streams of Alaska and Siberia, frozen part of the year, and the hot springs and stagnant pools of equatorial swamps all being inhabited by some forms of fish life. Many oceanic fish must also endure low temperatures, the deeper layers of the ocean being at most 3—4°F.

Table 7.

Catfish, 10 animals observed.

Heat contracture				
Beginning of heat contracture				
Temperature, °C.		% of maximum heat contracture		
Average	Range	Average	Range	
32.0	30.0—34.0	16	6 - 66	
Completion of heat contracture				
Temperature, °C.		Maximum heat contracture		
Average	Range	Average	Range	
39.0	38.0—40.0	75 mm.	20—91 mm.	

Magnification 8×. Load: 10 g.
Muscle length: Before heat contracture 36 mm. (average).
After completion of heat contracture 28 mm. (average).
Decrease of muscle length 22%.

Table 8.

Excitability (Catfish)

	(1)		(2)		(3)		(4)		(5)		(6)	
	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
Temperature °C.	17.2	15.0—20.0	20.5	18.5—22.0	23.6	22.0—24.5	25.2	23.5—26.0	28.2	26.0—30.0	30.0	28.0—32.5
Maximum tetanus mm.[1]	83	55—103	80.5	55—103	68	25—93	58	23—88	36.5	7—81	15.5	5—50
Percent of highest response in (1)	100		97		82		70		43		18.7	

$$\frac{\text{Maximum heat contracture}}{\text{Maximum tetanus}} = \frac{75}{83} \text{ or } 90\%$$

[1] Magnification 8×.

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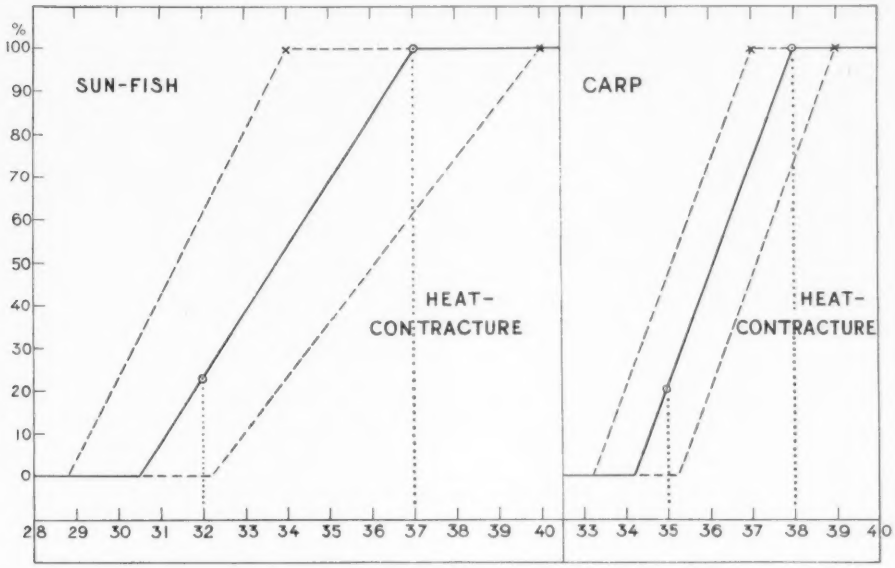

Fig. 5.

above freezing point, whereas coastal forms in South Africa live in water up to 120°F. The distribution of pelagic and coastal fishes corresponds remarkably closely to the temperature of the water (mean annual isotherms).

SIMPSON (17) examined the body temperature of marine fish, crustaceans and echinoderms and compared these with the temperature of the water in which they live. The mean temperature in the muscles of the codfish is 0.46°C. above the water temperature. AGERSBORG (18) observed a number

Table 9.

	Beginning of heat contracture				Completion of heat contracture			
	Temperature		% of maximum heat contracture		Temperature		Maximum heat contracture	
	Average °C.	Range °C.	Average	Range	Average °C.	Range °C.	Average	Range
Carp, 10 animals	35.0	34.0—36.0	20	5—56	38.0	37.0—39.0	18 mm.	4—80mm.
Sunfish, 6 animals	32.0	30.0—34.0	23	12.5—66.5	37.0	34.0—40.0	25.5 mm.	8—40mm.

Magnification 13×. Load: carp, muscle 10 g.
sunfish, muscle 4 g.

of fish species (gizzard-shad, crappies, bluegill, sunfish, chub, minnow, carp, catfish) attracted into a bay with a large amount of bottom food, its temperature kept between 28—30°C. by warm waste water from a starch factory. He states that as long as the temperature in the bay stays approximately the same the fish now adapted to the higher temperature thrive—except for the occasional death of a gizzard-shad. When the temperature is *suddenly* changed to the winter temperature of the reservoir, their natural habitat, all the fish that had become gradually accustomed to the abnormally high water temperature die. *Under natural (not influenced,) living conditions, these same species live through the winter in the cold reservoir perfectly well.* Even a *sudden decrease* of the bay temperature of 2°C. brought about symptoms of unbalanced movements. This is due to the inability of the fish to adapt themselves to *sudden* temperature changes, whereas gradual, slow changes can be met without trouble.

The temperature of the warm water bay was only a few degrees lower than the temperature at which the muscles of the fresh water types in the reported experiments began to start heat contracture and showed loss of muscular excitability. It must, however, be borne in mind that the investigated fish species were taken out of cold water, 8—10°C., to which they had adapted themselves. Muscles from fish, *gradually* acclimatized to live in water of higher temperature than natural living conditions provide, may conceivably show that adaptation in a later onset of heat contracture and a disappearance of muscular excitability at higher temperatures as compared with muscles from members of the same species which were adapted to lower temperatures before investigated.

From this it would follow that the power to adapt to temperature changes of the environment is well developed in fish, provided that these changes do not occur *suddenly*. A comparative study of the correlation between natural temperature conditions and the temperature susceptibility of the skeletal muscles must take that into account. VERNON (3) does not give the water temperature at which the goldfish and common eels were kept before his experiments. The loss of excitability occurs in his experiments at a higher temperature (39.3°C.), the heat contracture starts at a lower temperature (eel, 28.8°C.; goldfish, 33.4°C.), but culminates at a higher temperature (eel, 44.6°C.; goldfish, 41.8°C.) than in the experiments reported in this paper.

French scientists observed that eels (Anguilla vulgaris) started to fall into coma and convulsions at 41—42°C. and death occurred at 45—47°C. No data are given as regards the water temperature at which the eels were kept previously. HUNTSMAN and SPARKS (19) studied the temperatures at which death occurs in several species of marine fish.

The heat contracture of the dogfish muscles starts at a temperature 6°C. lower than that of the muscles of the conger eel. The dogfish is not a ground-

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fish, but may be found swimming at any depth. The temperature on the surface is, on the average, always a few degrees higher than at greater depth. The conger eel, on the other hand, prefers deeper waters. In the 4 fresh water species investigated, the muscles of the catfish show the widest range of temperature for heat contracture (7°C.) and the earliest cessation of muscular excitability. These fish stay near the bottom and move about slowly. The goldfish muscles have a range of only 2°C. and excitability in them disappears later, at a higher temperature. In general, goldfish naturally inhabit warmer waters, temperate and warm climate preferred. The carp, of the same family as the goldfish, but larger and to a certain extent more adapted to colder waters shows in its muscles a slightly wider range (3°C.).

Summary.

In six species of fish the onset and completion of the heat contracture and the excitability of the skeletal muscles in relation to various temperatures was comparatively studied. The data may be summarized as follows:

Species	Range of temperature for heat contracture °C.	Last muscle response observed, °C.	% of highest response
Dogfish	29—35	31.6	17
Catfish	32—39	30.0	18.7
Sunfish	32—37	—	—
Conger eel	35—38.5	33.7	14
Carp	35—38	—	—
Goldfish	37—39	34.0	11

I wish to express my appreciation to Professor J. A. DYE for his helpful criticisms which aided so much in the preparation of this manuscript.

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CYTOLOGICAL STUDY OF THE HETEROGENEOUS FERTILIZATION OF THE EGG OF RABBIT OUTSIDE THE ORGANISM

BY

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Contribution of the Histological Section of Temiriazev's Biological Institute (Chief of Section Prof. O. B. Lepeshinskaja).

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1. INTRODUCTION.

Under the term of the heterogeneous fertilization we mean the processes of fertilization of egg by the spermatozoon of an animal from another species, genus, or family. Heterogeneous fertilization may result in development of the hybrid embryo having the features of both parents, i.e. having hereditary signs belonging to distantly related species. The question of hybridization is not only of theoretical but also of practical importance, as it is connected with the production of new species of animals.

Hybridization of animals from different species was first attained with amphibia by PFLÜGER (1882) and by BORN (1883). They showed in number of cases that, though the fertilization of eggs by the sperm of animals of another species was possible the development of the egg did not go beyond the stage of blastula; while in case of hybridization of more closely related species the development of the embryo sometimes reached metamorphosis. The questions of hybridization have attracted the attention of scientists and the possibility of heterogeneous fertilization was studied in detail on the eggs of animals with extreme fertilization, as in case of echinodermata, bony

fishes and amphibians (LILLIE, 1925). It was stated that specifity may be displayed at different stages of fertilization. At hybridization of distantly related animals the eggs either did not react with the heterogeneous spermatozoon, or the spermatozoa, though causing cortical changes, did not enter the egg. On the other hand, if spermatozoa sometimes got into the egg and were fused with the egg nucleous, they could be secondarily eliminated at the first, or posterior cleavage. These facts show the difference in impediments to the heterogeneous fertilization in different cases. DONCASTER and GRAY carried out (1913) the cytological study of eggs in case of hybridization of sea-urchins of different species. In the experiments which they describe, only some hybrid combinations have given normally developing hybrids; in those cases where the development of the egg did not occur the authors observed either the elimination of chromosomes of the first spindle of cleavage, or the gathering of the changed chromosomes without cleavage at one pole in compact mass. The heterogeneous fertilization of mammals has not yet been studied because of the difficulty to obtain their eggs and their small dimensions.

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The application of artificial insemination allows to carry out the hybridization of mammals on a greater scale, but it is not always possible to obtain fertilization by means of artificial insemination. This depends on two causes: either the spermatozoon perishes in the new medium into which it is brought, or the eggs and the spermatozoon are so biologically heterogeneous cells, that their fusion is impossible. These difficulties of heterogeneous insemination point to the necessity of studying the process of fertilization of mammals outside the organism. Placing the eggs and spermatozoa into the drop of plasma we are able to observe directly the behaviour of egg and spermatozoa. PINCUS (1930, 1932), LEWIS and GREGORY (1929), GREGORY (1930), GILCHRIST and PINCUS (1933), KRASOVSKAJA and DIOMIDOVA (1934), LEWIS and HARTMAN (1933), KRASOVSKAJA (1934, 1935) have applied this method of study of the fertilization and cleavage of eggs of mammals outside the organism. As to the question of the heterogeneous fertilization of mammals, we have no studies except the observations of JAMANE (1930), who carried out the insemination of the rabbit egg by the spermatozoa of rat and horse outside the organism and observed in both cases the issue of the second polar body. It is a pity, that JAMANE did not procede with his observation and now we have no data to solve the problem, whether the heterogeneous fertilization was attained in these experiments or not.

Having studied the fertilization outside the organism and the early stages of cleavage of the rabbit egg, we thought it necessary to pass to the study of the heterogeneous fertilization outside the organism, applying the methods which were worked out in our previous experiments.

2. MATERIAL AND METHOD OF STUDY.

As material for this investigation there were used the eggs of rabbit obtained 17 hours after copulation with vasectomised male. We have described in detail the technique of obtaining the eggs in the 1st (KRASOVSKAJA and DIOMIDOVA, 1934) and the 2nd (KRASOVSKAJA, 1934) contributions. The method to obtain the spermatozoa was as follows: by means of an operation the testicle was taken out from animal. After cutting the films the spermatozoa were squeezed out from the epidydimis by means of a thin pincher and were mixed with Ringer's solution. Rather thick suspension of spermatozoa was prepared in all series. As it was noticed that the plasma effects the influence upon the motion of spermatozoa, we left the eggs with spermatozoa during 20 minutes and then added to the egg a drop of the rabbit blood plasma. The egg placed inside, the drop according the type of hanging drop was put into thermostate at 37°C. The eggs were under observation during 24 hours. The different stages of the development of eggs were drawn while they were alive by means of Zeiss' drawing apparatus and then the eggs were fixed.

The observations of the living eggs were checked by the cytological investigations. For fixation of the eggs we used the solutions of ZENKER, BOUIN and NOVAC. The eggs were placed in paraffin and then were cut into series of fine sections 8 μ thick. They were stained either by iron haematoxylin, or the complicate staining by safranine-picro-indigo-carmine was used.

3. INSEMINATION OF THE RABBIT EGG BY THE SPERMATOZOON OF WHITE RAT.

Having investigated the process of fertilization of egg by the spermatozoon of rabbit we have made a series of experiments to study the heterogeneous fertilization of the rabbit eggs by the spermatozoon of white rat. Observations were carried out on 49 eggs. Soon after the insertion of eggs and spermatozoa into the plasma, the dilution of the plasma around the egg was observed, what served as a certain indirect argument that in this case a cortical reaction had taken place. Studying the fertilization of eggs of rabbit by the rabbit spermatozoa, I have noted the variation of fermentative influence of cortical layer of egg upon the surrounding plasma. I observed also, as a constant phenomenon, the dilution of the plasma around the fertilized eggs, while around the unfertilized egg the dilution of plasma was never noticed (KRASOVSKAJA, 1934). In the zone of dilution around the eggs of

rabbit, one could observe the motion of the rat spermatozoa towards the surface of egg during one hour, while in the clot of plasma the spermatozoa remained immovable. I have not observed the penetration of the spermatozoon into the egg, but in course of 1—2 hours after addition of spermatozoa to the egg there was noticed the issue of the second polar body. It is known that in the egg of rabbit the issue of the second polar body takes place after the penetration of the spermatozoon into the egg (JAMANE, 1930, KRASOVSKAJA and DIOMIDOVA, 1934). 5—6 hours after the addition of spermatozoa the formation of two pronuclei was noticed in the eggs. This coincides in time with the progress of fertilization of the rabbit eggs outside the organism (KRASOVSKAJA, 1934). In some eggs one could observe the removal of the pronuclei to the centre of the egg. Simultaneously with the shifting of the pronuclei grew the dimensions of eggs. This fact is characteristic for this stage of their development. 15—16 hours after the addition of spermatozoa to the egg, the cleavage of eggs was observed. The process of cleavage was of the same type as described at the fertilization of the egg of rabbit by the rabbit spermatozoon (KRASOVSKAJA, 1934). The first cleavage furrow begins from the side of the polar bodies and gradually extends to the meridian of the egg, dividing it into two cells. The cleavage of the egg continues 15—20 minutes.

Working with stained preparations we observed two polar bodies (Fig. 1). In the centre of the egg one could discover two pronuclei (Fig. 2), which, as it seems, did not differ in any respect from the pronuclei of the rabbit egg, except that one pronucleus was sometimes smaller than the other. In 75 % of cases we observed the division of the egg into two blastomeres. There is shown in Fig. 3 the egg at the stage of two blastomeres, which have the nuclei not differing by their dimensions from the nuclei of the rabbit egg. The nucleus in the right blastomere on the microphotogram is indistinct because the greater part of the nucleus has got into the neighbouring section. This egg had two polar bodies. One egg was discovered at the stage of three blastomeres (Fig. 4). Examining the series of sections it was possible to see the nuclei in all three blastomeres. In the protoplasma of eggs inseminated by the spermatozoa of rat I noted the presence of drops of different size, intensively stained by EH in black color what was not appropriate to the rabbit eggs. Very interesting is the fact that the similar granularity in the fertilized eggs of rat was described by KREMER (1926). It seems that the appearance of this granularity is connected with the penetration of the rat spermatozoon into the egg of rabbit.

The cytological study of eggs, remaining in the unicellular stage has shown different declinations in the development. The pronuclei in fertilized eggs of rabbit have always oval form. In some eggs after their insemination by the spermatozoa of rat we have discovered the pronuclei of irregular shape and

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having projections (Fig. 5). In the other case the egg had only one pronucleus, in which the part of chromatin was in compact mass, while behind the nucleus membrane it was possible to observe the isolated little blocks of chromatin (Fig. 6). Sometimes even 4 pronuclei could be observed in the centre of egg (Fig. 7). We cannot say whether we had here the penetration into the egg of several spermatozoa which produced the formation of several pronuclei, or it was the constriction of two previously formed pronuclei. In Fig. 8 there is one egg the development of which has stopped at the stage of two blastomeres. Comparing it with Fig. 2 it becomes clear, that these blastomeres have degenerative nuclei, which are laced into several little nuclei forming a sort of a chain. Thus on the basis of observations of the living eggs and the cytological study we come to the following conclusion: at insemination of the egg of rabbit by the rat spermatozoon we have in 75 % of cases the penetration of spermatozoon, the issue of the second polar body, the formation of pronuclei and cleavage of the egg into two blastomeres (in one case—into 3 blastomeres). In 25 % of cases the cleavage of eggs does not occur, and this, as it appears, is connected with different declinations in development at the heterogeneous fertilization.

4. INSEMINATION OF THE RABBIT EGG BY THE SPERMATOZOON OF GUINEA PIG.

In this series of experiments there were studied 16 eggs. First observation showed that the eggs are surrounded by the cells of follicular epithelium and have the first polar body. The spermatozoa had been lively shifting around the eggs until the protoplasma was added, when their movement somewhat stopped. Observing the eggs two hours after the beginning of study I paid attention to the egg No. 2. It diminished in size because two little balls of protoplasma lying in periovular space near the guiding corpuscles divided from it. Eight hours after the addition of spermatozoa we observed two pronuclei in the centre of this egg and the fact served as an argument, that constricting out of protoplasma had not been the sign of degenerative variation. The egg was fixed in this stage. Cytological study showed that the egg was at the stage of two pronuclei, but in periovular space, except the polar bodies lay the balls of protoplasma (Fig. 9). This phenomenon of separation of the part of protoplasma was first described by VAN-DER-STRICHT (1909) on the eggs of bat under the name of deutoplasmolysis and later by LAMS (1913) on the eggs of guinea pig. These authors think that deutoplasmolysis consists in appearance of numerous buds on the surface of egg, numbers of buds being different, some of which may separate and exist in free state in the peri-

ovular space near the polar bodies. This process of deutoplasmolysis particularly displayed after the issue of the second polar body and in the stage of the spindle of cleavage. VAN-DER-STRICHT has observed deutoplasmolysis on all eggs of bat and has accepted it as phenomenon proper to the normal development of these eggs. On the unfertilized eggs he never observed any traces of deutoplasmolysis. Lams often found deutoplasmolysis in guinea pig and considered it as a constant phenomenon proper to the eggs of guinea pig. The fragmentation of protoplasma in this series of experiments may be accepted as deutoplasmolysis, occuring in result of some action of the guinea pig spermatozoon upon the egg of rabbit.

In process of observation it was discovered that the radius of dilution of the plasma around the egg was smaller comparing with the dilution of the plasma around the fertilized rabbit eggs. Thus, it appears, that the cortical layer of egg has weaker proteolytic action upon the surrounding plasma. The presence of two pronuclei serves as indirect argument that the spermatozoon of guinea pig has penetrated into the egg of rabbit, but we have not been able to observe the cleavage of the eggs. However, I have twice observed the egg in the stage of two cells, but it has been hard to decide whether it was the actual cleavage, or deutoplasmolysis. In any instance here is the description of these cases. In course of the study of the living eggs No. 6 from the experiment No. 62 the pronuclei were not discovered. After fixation one could observe on series of sections, that the egg somewhat divided into two parts, the nucleus being only in one cell and having degenerative character, reminding the picnosis of nucleus (Fig. 10). There were many little balls of the protoplasma in the periovular space. Separation of little balls of protoplasma and its division into two parts one could see particularly well on the neighbouring section (Fig. 11). But the presence of the degenerative nucleus only in one cell and existance of a great number of little balls of protoplasma in the periovular space argue more in favour of deutoplasmolysis, than in favour of cleavage. Somewhat another picture presented the egg No. 7 from the same experiment. It also had no pronuclei at the unicellular stage, but 18 hours after addition of the spermatozoa to the egg, the latter was discovered at the stage of two cells, the nucleus existing only in one cell (Fig. 12). Two polar bodies and several little balls of protoplasma lay in the periovular space (Fig. 13). In some eggs I have observed the stage of two pronuclei. Little balls of protoplasma lay in the periovular space of the majority of eggs and it was difficult to decide on the basis of observations of living eggs. Whether the polar bodies were glistening through, or we met with some new formations. The cytological study has given the complete explanation to this phenomenon. The majority of the eggs of rabbit inseminated by the spermatozoa of guinea pig have desplayed the phenomenon of deutoplasmolysis. It is true, that the phenomenon of deutoplasmolysis claims the additionary study on

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wide material, but these observations allow to suppose that the cause of deutoplasmolysis lies in the spermatozoon of the guinea pig. When the eggs of rabbit were inseminated either by the spermatozoa of rabbit or by the spermatozoa of rat, the phenomenon of deutoplasmolysis was never observed. Thus the observation of living eggs and the cytological study give such incongruent picture, that it is difficult to say whether we actually have the fertilization in this case.

5. INSEMINATION OF THE RABBIT EGG BY THE SPERMATOZOON OF DOG.

Having studied the heterogeneous fertilization in one family of rodents we were interested to observe the behaviour of sexual cells, taken from the more distantly related animals. With this purpose we have undertaken the series of experiments on the hybrid fertilization of the egg of rabbit by the spermatozoon of dog. We thought that in this case the fertilization could not occur, but supposed that the spermatozoon of dog might serve as an stimulizing agent for the parthenogenetic development of the egg of rabbit. Applying our usual method we have placed the egg of rabbit into the plasma together with the spermatozoa of dog. In this series of experiments we have studied 13 eggs. The observations of eggs began 3 hours after they had been placed into the plasma. At examination it occured, that the plasma around the eggs was not deluted. It was an argument in favour of absence of the cortical reaction in this case. Neither could we discover the issue of the second polar body. The measurement of the eggs during further observations showed that the size of the eggs did not change. In our previous works we stated, that the size of egg at the unicellular stage was not constant, but changed depending on the stage of development (KRASOVSKAJA, 1935). Thus the constant size of the eggs in this case, serves as the indirect argument that the development of the eggs did not occur. Usually 5—6 hours after the addition of the spermatozoa we observed in the egg the formation of two pronuclei. But in this series of experiments the formation of the pronuclei was never observed. It is true, that in the egg No. 7, seven hours after its insertion into the plasma, there was noticed the presence of two round formations, the character of which was quite incomprehensible. At the same time it was discovered that the protoplasma of the eggs had become large-grained and that the little cavities had appeared in it. The further study did not show the growth of volume of this egg, characteristic for the stage of the spindle of cleavage.

When this egg was observed 20 hours later, it was in the stage of two cells, noted above round formations being present in protoplasma. The cytological study of the fixed eggs has shown, that the eggs after their insemination by the spermatozoa of dog remained unfertilized, and we could trace the degenerative variations of the unfertilized egg. Such egg in the stage of one polar body is shown in Fig. 14. The neighbouring section shows the mitosis of the second polar body. The achromatin threads were dissolved and disappeared. The little vacuoles could be noticed in the protoplasma of this egg. Gradually the spindle of maturation passed nearer to the centre of the egg, where we discovered the little blocks of chromatin (Fig. 15). It appears that after the breaking of the achromatin figure the chromosomes are densified and clued together and therefore we find the compact mass of chromatin in the centre of the egg. Analogous variations of the unfertilized egg were described by Lams (1913) in guinea pig and by Sobotta (1896) in the eggs of the mouse. The variations of the egg No. 7, being incomprehensible during the observations in the living state, became quite clear after the cytological study of this egg (Fig. 17). The egg divided into two cells, having no nuclei and at the same time the areas of the large-grained plasma were discovered on the poles. May we take the described case of the egg No. 7 for cleavage? The absence in the egg of any variations characteristic for the process of fertilization as the cortical reaction, the issue of the second polar body, the formation of pronuclei, the secondary growth of the egg at the stage of the spindle of cleavage—allow us to suppose that in this case we have the simple constriction of the protoplasma of the egg. Thus on the basis of observation of living eggs and the cytological study we think that the spermatozoon of dog has neither penetrated into the egg of rabbit, nor appeared the stimulating agent helping to the development of the egg.

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6. DISCUSSION OF THE HETEROGENEOUS FERTILIZATION QUESTION.

Thus to study the heterogeneous fertilization we have made three series of experiments dealing with insemination of the rabbit egg by the spermatozoa of rat, guinea pig and dog. The egg of rabbit reacted differently at addition of different spermatozoa. The most favourable results have been obtained with insemination of the rabbit egg by the spermatozoa of rat, when we have been able to observe the cortical reaction, the issue of the second polar body, the presence of two pronuclei in the egg, the growth of the egg at the stage of the spindle of cleavage and the gradual formation of the furrow of cleavage. All this corresponds to the normal process of fertilization

of the rabbit egg. In 75 % of cases we observed the cleavage of egg. In 25 % of cases the cleavage did not occur in connection with different declinations in the development of the egg. When the rabbit egg was inseminated by the spermatozoa of guinea pig we observed quite another reaction from the egg, i.e. the cortical reaction was expressed weaker. We observed two pronuclei in the eggs but could not notice the growth of eggs at the unicellular stage. The cleavage of the given eggs was not observed. One could note the deutoplasmolysis of the eggs, as a constant phenomenon. These observations allow us to suppose that the deutoplasmolysis of the rabbit eggs occurred under the influence of the spermatozoa of guinea pig. After the insemination of the eggs of rabbit by the spermatozoa of dog we did not observe any signs of fertilization, but had the degenerative variations of the unfertilized egg. The fact, that the egg reacted in different ways after addition of different spermatozoon allows to suppose that the given hybrid combinations display the different modifications of specifity in the fertilization. We have not observed the penetration of the spermatozoon into the egg, and may only suppose, that at the insemination by the spermatozoa of rat the heterogeneous fertilization has taken place. For this supposal and against the parthenogenesis speak the variations of the egg which we have observed at the unicellular stage. The variations observed were quite similar to those ones, which we had investigated at the normal fertilization of the egg of rabbit. The presence of the nuclei in the blastomeres is also a positive argument in favour of fertilization, these nuclei being of the same size with the nuclei observed at normal fertilization of the rabbit egg. These experiments give no foundation to think that the spermatozoa of an animal from the distant species cannot stimulate the rabbit egg. It is possible that, if we take a heavier sperm suspension, or change the conditions of culture of the egg, we shall be able to observe the activiation to the development of egg.

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DESCRIPTION OF THE FIGURES IN TEXT.

PLATE I.

Fig. 1. The egg of rabbit inseminated by the spermatozoa of rat. In the periovular space lie two polar bodies. In the protoplasma there are one pronucleus and drops stained by EH in black color.

Fig. 2. The egg of rabbit after insemination by the spermatozoa of rat. Two pronuclei lie in the centre of the egg.

Fig. 3. The egg of rabbit after insemination by the spermatozoa of rat is at the stage of two blastomeres. There are nuclei in both cells.

Fig. 4. The egg of rabbit after insemination by the spermatozoa of rat is at the stage of 3 blastomeres. There are nuclei in two blastomeres.

Fig. 5. The rabbit egg inseminated by the spermatozoa of rat is at the stage of two pronuclei of irregular form and having projections.

Fig. 6. The rabbit egg inseminated by the spermatozoa of rat having one pronucleus, the chromatin of the egg lying in compact mass. Little blocks of chromatin are lying in the protoplasma near the membrane of the nucleus, as well as the drops stained by EH in black colour.

Fig. 7. The rabbit egg inseminated by the spermatozoa of rat having 4 pronuclei in its centre.

Fig. 8. The rabbit egg inseminated by the spermatozoa of rat is at the stage of two blastomeres having devided nuclei.

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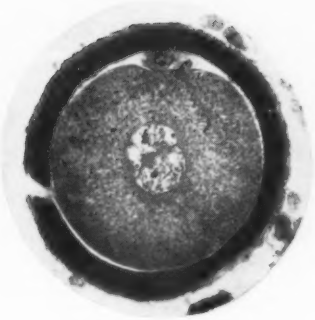

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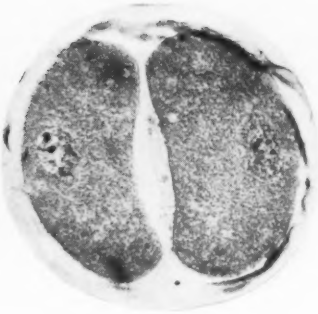

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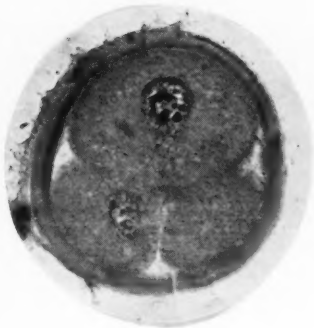

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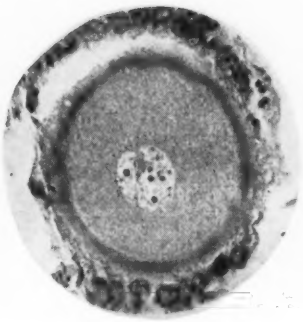

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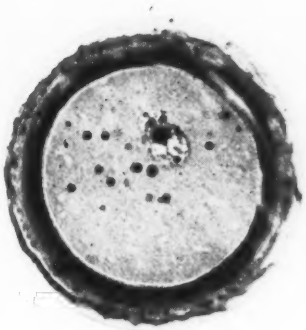

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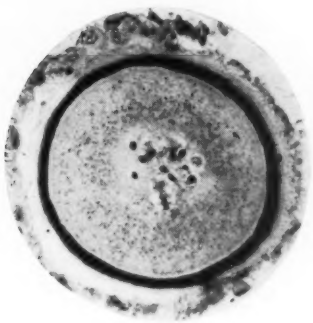

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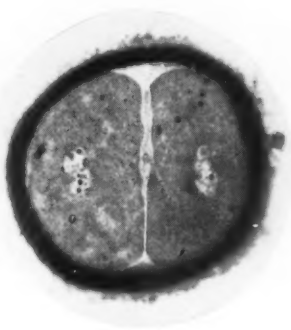

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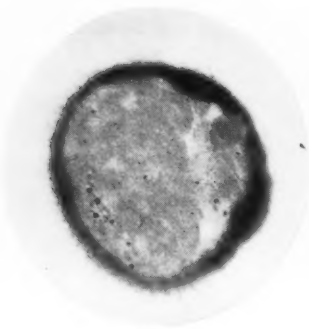

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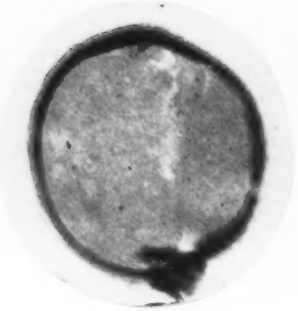

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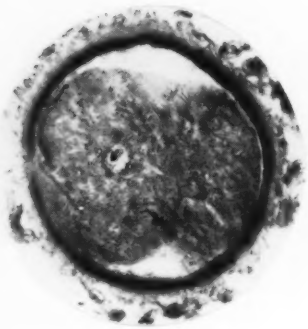

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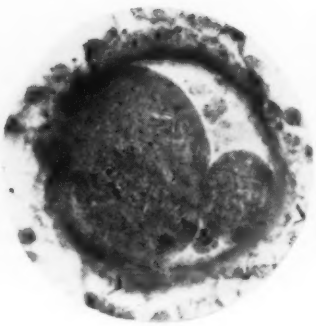

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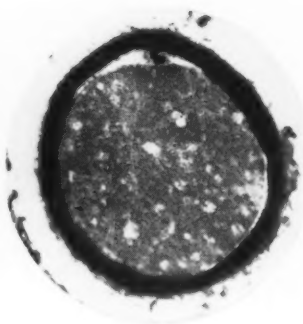

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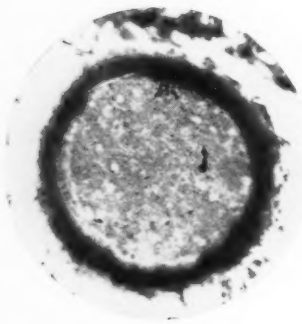

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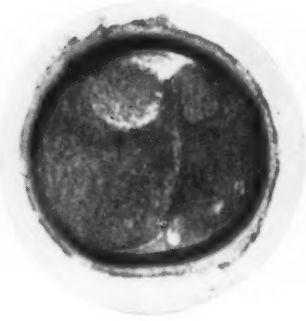

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PLATE II.

Fig. 9. The rabbit egg inseminated by the spermatozoa of guinea pig. The egg is at the stage of two pronuclei. Little balls of protoplasma are lying in the periovular space, except the polar bodies.

Fig. 10. The rabbit egg inseminated by the spermatozoa of guinea pig. The egg has undergone the division into two cells, one having the degenerative nucleus and the other having no nucleus. The little balls of chromatin lie in the periovular space.

Fig. 11. The same egg (the neighbouring section). Two cells without nuclei and little balls of protoplasma are lying in the periovular space.

Fig. 12. The rabbit egg inseminated by the spermatozoa of guinea pig. The egg is at the stage of two cells, one of the cells having a nucleus.

Fig. 13. The same egg (the neighbouring section), two cells without nuclei and little balls of protoplasma lying in the periovular space.

Fig. 14. The rabbit egg inseminated by the spermatozoa of dog. The egg is at the stage of the first polar body. There are vacuoles in the protoplasma.

Fig. 15. The same egg (the neighbouring section), the spindle of the second maturation lying in the periphery of the egg.

Fig. 16. The rabbit egg after insemination by the spermatozoa of dog, the blocks of chromatin lying in the centre of the egg. There are larger vacuoles in the protoplasma of the egg.

Fig. 17. The rabbit egg after insemination by the spermatozoa of dog. The egg is at the stage of two cells, which have no nuclei. The protoplasma on the poles of the blastomeres is degeneratively changed.